

# A NEW OLIGOCENE-MIOCENE SPECIES OF *BURRAMYS* (MARSUPIALIA, BURRAMYIDAE) FROM RIVERSLEIGH, NORTHWESTERN QUEENSLAND

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*Burramys* is abundant in the Oligocene-Miocene at Riversleigh, northwestern Queensland. *Burramys brutyi* sp. nov. is represented by over 150 dentary and maxillary fragments and isolated teeth from 22 sites. *Burramys* appears to be morphologically conservative, with only minor metrical variation between specimens of *B. brutyi* from different sites and relatively few features distinguishing Miocene, Pliocene and Recent species. Phylogenetic analyses suggest that *B. brutyi* is the plesiomorphic sister-group to all other species of *Burramys*, with *B. wakefieldi* sister-group to the clade comprising *B. triradiatus* and *B. parvus*. □  
*Burramyidae, Burramys brutyi, Riversleigh, Oligocene, Miocene.*

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*Burramys* was represented only by Pleistocene fossils of *B. parvus* from Wombeyan Caves, NSW (Broom, 1896) and Pyramids Cave, Victoria (Wakefield, 1960) until 1966 when the Mountain Pygmy-possum, *B. parvus*, was discovered alive at Mount Hotham, Victoria (Anon., 1966; Warneke, 1967). Two more fossil species of *Burramys* have been identified: early Pliocene *B. triradiatus* from Hamilton, Victoria (Turnbull et al., 1987) and *B. wakefieldi* from late Oligocene (Woodburne et al., 1993) Ngama Local Fauna, South Australia (Pledge, 1987). Discovery of Miocene *Burramys* at Riversleigh extends the geographic range far north and provides the first sizeable Tertiary sample (150 specimens). A metric analysis of this sample aims to determine taxa present and to assess variation. *Burramys brutyi* sp. nov. is used as the basis for an evaluation of intrageneric phylogenetics of *Burramys*.

Dental homology follows Flower (1867) for premolar numbering and Lockett (1993) for premolar/molar boundary and molar number. Tooth positions given without super- or subscript numbers refer to both upper and lower teeth: thus M<sup>1</sup> and M<sub>1</sub> are individual teeth but M4 refers to both. Molar cusp nomenclature follows Archer (1984) not Pledge (1987). Pledge's paraconid is our protoconid; his protoconid is not recognised.

Higher systematic nomenclature follows Aplin & Archer (1987). System nomenclature is based on Archer et al. (1989) and Creaser (1997). Material referred to is housed in the Queensland Museum, Brisbane (QMF) or Museum of Victoria, Melbourne, (NMVP). Measurements in millimetres (mm) are to the nearest 0.01 mm using a Wild MMS235 Digital Length-Measuring Set

attached to a Wild M5A stereomicroscope. Molar lengths and widths and molar row lengths were measured as the maximum dimensions of the enamel-covered crown(s) with the teeth in occlusal view, with lengths taken along the anteroposterior axis of the tooth and widths measured perpendicular to that axis. For P<sub>3</sub> in dorsal view and P<sup>3</sup> in ventral view, maximum length was measured parallel to the apical blade edge, and anterior, posterior and maximum widths were measured perpendicular to the blade edge; buccal and lingual heights were measured from the base of the enamel at the saddle between the roots, to the median apical edge, parallel to the posterior edge of the tooth. Statistical analyses were performed using SYSTAT and Kaleida-Graph data analysis and graphics applications.

## METRIC ANALYSIS

Despite overall uniformity, Riversleigh *Burramys* material shows some variation in relative and absolute premolar and molar sizes. Metric analysis of dental features attempted to identify patterns which might indicate sexual dimorphism, specific or subspecific separation or differentiation of populations from different sites. Univariate and bivariate distributions and principal components analysis were employed.

Cheektooth dimensions (Table 1) for Recent *B. parvus* populations refer to left dentition except where the right dentition was more complete. Standard error (SE) is used rather than standard deviation (SD) because it better indicates reliability of the mean estimate. The coefficient of variation (CV)= SD divided by mean  $\times$  100.

TABLE 1. Cheektooth dimensions of *Burramys* species. Results given as: Mean  $\pm$  Standard Error (No. Specimens) Coefficient of Variation (CV%). CV not given where n  $\leq$  2. L = length, AW = anterior width, PW = posterior width, MW = maximum width, LH = lingual height, BH = buccal height.

	Riversleigh <i>Burramys</i>		<i>B. wakefieldi</i>		<i>B. triradiatus</i>		<i>B. parvus</i>	
		CV		CV		CV		CV
<i>Lower teeth</i>								
P <sub>3</sub> L	1.81 $\pm$ 0.01 (38)	4.00	1.64	(1)	2.58 $\pm$ 0.05 (4)	3.68	2.17 $\pm$ 0.01 (21)	1.96
P <sub>3</sub> AW	1.03 $\pm$ 0.01 (38)	8.21	0.86	(1)	1.04 $\pm$ 0.01 (4)	1.85	0.85 $\pm$ 0.02 (21)	10.51
P <sub>3</sub> PW	1.22 $\pm$ 0.01 (38)	5.07	1.22	(1)	1.49 $\pm$ 0.06 (4)	7.96	1.32 $\pm$ 0.01 (21)	4.11
P <sub>3</sub> MW	1.27 $\pm$ 0.01 (29)	5.58	1.22	(1)	1.67 $\pm$ 0.06 (4)	6.61	1.39 $\pm$ 0.02 (21)	4.79
P <sub>3</sub> LH	1.44 $\pm$ 0.01 (37)	5.25	1.29	(1)	2.02 $\pm$ 0.04 (4)	3.73	1.92 $\pm$ 0.01 (19)	3.23
P <sub>3</sub> BH	1.73 $\pm$ 0.02 (37)	5.64	1.51	(1)	2.44 $\pm$ 0.05 (4)	3.98	2.22 $\pm$ 0.02 (20)	3.05
M <sub>1</sub> L	1.24 $\pm$ 0.01 (32)	3.71	1.21	(1)	-	-	1.57 $\pm$ 0.01 (21)	2.02
M <sub>1</sub> AW	0.78 $\pm$ 0.01 (32)	7.89	0.86	(1)	-	-	1.00 $\pm$ 0.01 (21)	4.23
M <sub>1</sub> PW	0.95 $\pm$ 0.01 (32)	5.80	0.97	(1)	-	-	1.25 $\pm$ 0.01 (21)	3.60
M <sub>2</sub> L	1.09 $\pm$ 0.01 (32)	3.72	-	-	1.55	(1)	1.57 $\pm$ 0.01 (21)	1.97
M <sub>2</sub> AW	0.88 $\pm$ 0.01 (34)	5.55	-	-	1.23	(1)	1.21 $\pm$ 0.01 (21)	2.03
M <sub>2</sub> PW	0.96 $\pm$ 0.01 (34)	5.67	-	-	1.32	(1)	1.32 $\pm$ 0.01 (21)	1.90
M <sub>3</sub> L	0.93 $\pm$ 0.02 (10)	6.48	-	-	1.32 $\pm$ 0.04 (2)	4.29	1.23 $\pm$ 0.01 (19)	1.84
M <sub>3</sub> AW	0.84 $\pm$ 0.01 (10)	4.46	-	-	1.13 $\pm$ 0.00 (2)	0.00	1.06 $\pm$ 0.01 (19)	2.25
M <sub>3</sub> PW	0.85 $\pm$ 0.02 (10)	6.13	-	-	1.17 $\pm$ 0.01 (2)	0.61	1.07 $\pm$ 0.01 (19)	2.76
M <sub>4</sub> L	0.66	(1)	-	-	-	-	0.68 $\pm$ 0.01 (14)	5.88
M <sub>4</sub> AW	0.64	(1)	-	-	-	-	0.66 $\pm$ 0.01 (14)	6.83
M <sub>4</sub> PW	0.50	(1)	-	-	-	-	0.52 $\pm$ 0.01 (14)	7.82
M <sub>1-2</sub>	2.30 $\pm$ 0.02 (27)	3.37	-	-	-	-	3.13 $\pm$ 0.01 (21)	1.96
M <sub>1-3</sub>	3.24 $\pm$ 0.05 (8)	3.91	-	-	-	-	4.34 $\pm$ 0.01 (19)	1.34
M <sub>1-4</sub>	3.83	(1)	-	-	-	-	4.93 $\pm$ 0.02 (14)	1.29
<i>Upper teeth</i>								
P <sup>3</sup> L	2.01 $\pm$ 0.02 (17)	4.89	-	-	2.59 $\pm$ 0.02 (2)	1.09	2.27 $\pm$ 0.01 (19)	2.60
P <sup>3</sup> AW	0.93 $\pm$ 0.01 (17)	4.32	-	-	0.91 $\pm$ 0.02 (2)	2.32	0.75 $\pm$ 0.02 (19)	10.39
P <sup>3</sup> PW	1.20 $\pm$ 0.01 (17)	4.93	-	-	1.63 $\pm$ 0.05 (2)	4.79	1.13 $\pm$ 0.01 (19)	3.82
P <sup>3</sup> MW	1.25 $\pm$ 0.01 (17)	4.41	-	-	1.63 $\pm$ 0.05 (2)	4.79	1.24 $\pm$ 0.01 (19)	2.44
P <sup>3</sup> LH	1.58 $\pm$ 0.02 (17)	4.67	-	-	2.32 $\pm$ 0.02 (2)	1.22	1.92 $\pm$ 0.01 (16)	2.76
P <sup>3</sup> BH	1.65 $\pm$ 0.02 (17)	4.44	-	-	2.16 $\pm$ 0.01 (2)	0.98	2.06 $\pm$ 0.02 (18)	3.08
M <sup>1</sup> L	1.12 $\pm$ 0.02 (14)	4.86	-	-	-	-	1.51 $\pm$ 0.01 (19)	1.94
M <sup>1</sup> AW	1.16 $\pm$ 0.02 (14)	5.25	-	-	-	-	1.40 $\pm$ 0.02 (19)	7.08
M <sup>1</sup> PW	1.17 $\pm$ 0.01 (14)	4.14	-	-	-	-	1.45 $\pm$ 0.01 (19)	4.01
M <sup>1</sup> MW	1.39 $\pm$ 0.01 (14)	3.90	-	-	-	-	1.68 $\pm$ 0.01 (18)	2.77
M <sup>2</sup> L	0.98 $\pm$ 0.01 (8)	3.45	-	-	1.22	(1)	1.45 $\pm$ 0.01 (19)	1.53
M <sup>2</sup> AW	1.16 $\pm$ 0.01 (8)	2.84	-	-	1.34	(1)	1.56 $\pm$ 0.01 (19)	2.20
M <sup>2</sup> PW	0.93 $\pm$ 0.01 (8)	2.40	-	-	1.10	(1)	1.27 $\pm$ 0.01 (19)	3.37
M <sup>3</sup> L	0.86 $\pm$ 0.03 (3)	6.43	-	-	-	-	1.09 $\pm$ 0.02 (18)	8.17
M <sup>3</sup> AW	0.93 $\pm$ 0.02 (3)	2.84	-	-	-	-	1.19 $\pm$ 0.03 (18)	10.83
M <sup>3</sup> PW	0.72 $\pm$ 0.03 (3)	7.86	-	-	-	-	0.88 $\pm$ 0.02 (18)	10.71
M <sup>4</sup> L	0.67 $\pm$ 0.02 (3)	5.68	-	-	-	-	0.77 $\pm$ 0.01 (13)	4.86
M <sup>4</sup> AW	0.71 $\pm$ 0.02 (3)	4.97	-	-	-	-	0.74 $\pm$ 0.02 (13)	8.81
M <sup>4</sup> PW	0.46 $\pm$ 0.03 (3)	10.80	-	-	-	-	0.51 $\pm$ 0.01 (13)	9.49
M <sup>1-2</sup>	2.11 $\pm$ 0.03 (8)	3.40	-	-	-	-	2.96 $\pm$ 0.01 (19)	1.85
M <sup>1-3</sup>	2.98 $\pm$ 0.08 (3)	4.55	-	-	-	-	4.07 $\pm$ 0.02 (18)	1.63
M <sup>1-4</sup>	3.55 $\pm$ 0.03 (3)	1.33	-	-	-	-	4.77 $\pm$ 0.03 (13)	1.86

CV is less than 11 throughout and usually less than 6 (Table 1). Following Simpson et al. (1960), this degree of variation indicates an unmixed sample, although Gingerich (1974) cautions against uncritical application of this absolute CV criterion and recommends greater emphasis on relative variabilities of different teeth. In approx-

imately 80% of measurements *B. parvus* has a lower CV than the Riversleigh sample, but the interspecific differences in CV are generally not great. CVs for *B. triradiatus* fall within approximately the same ranges as those for the Riversleigh and Recent specimens, but are derived from very few specimens and are therefore

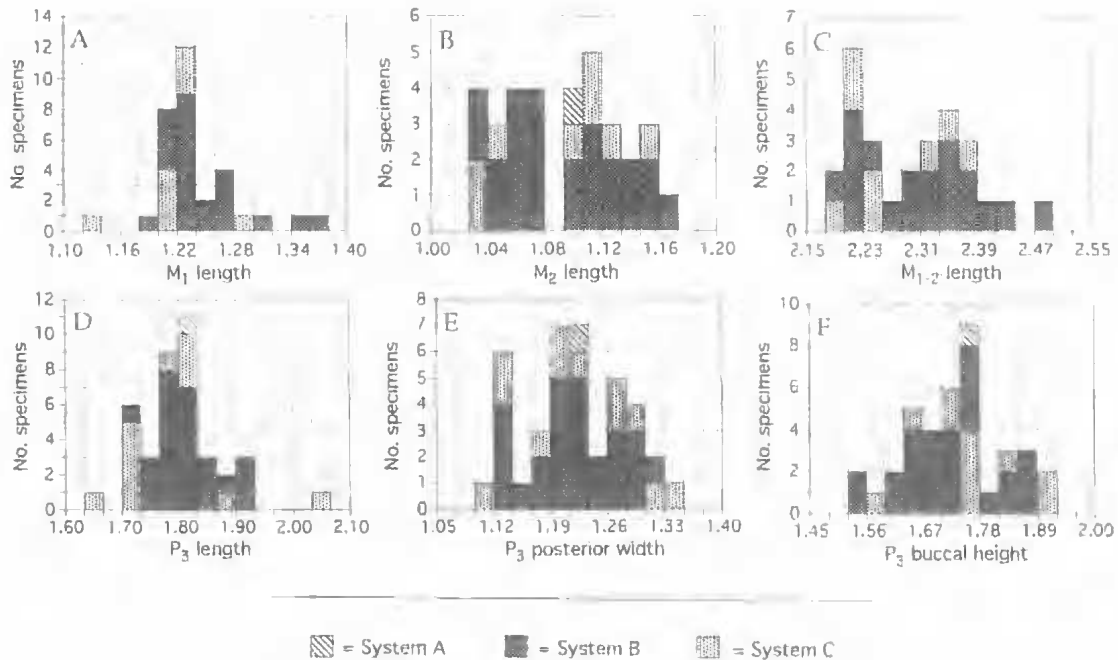


FIG. 1. Frequency histograms for some lower tooth measurements of Riversleigh *Burramys* specimens. All measurements in mm.

not considered reliable. Total variation (as indicated by CVs) suggests 1 species of *Burramys* in the Riversleigh sample spanning greater variation than the sample of Recent *B. parvus*.

Where variation between taxa is small (as is likely with small-bodied taxa), it may be obscured by epigenetic morphological variation, by tooth wear or by measurement error; metric differences between closely related taxa are most likely to be detected by examining structures with the lowest levels of such variation.  $M_2$ , in the centre of the  $P_3$ - $M_4$  tooth row, is in that sense the most functionally integrated of these teeth; it may therefore be expected to be least variable (Gingerich, 1974). Similarly, total molar row lengths may be more tightly controlled than the lengths of individual molars.  $M_2$  dimensions and molar row measurements (including partial molar row measurements such as  $M_{1-2}$  length) are generally the least variable measurements in *B. parvus* and the Riversleigh sample;  $P_3$  length is also relatively constant (Table 1). Thus analysis of the Riversleigh sample was focused on  $P_3$  and  $M_{1-2}$ , although all other measurements were examined.

Frequency histograms for some measurements are bimodal, while others are either unimodal or perhaps incipiently bimodal.  $M_{1-2}$  length (Fig.

1C), with  $CV=3.37$  is bimodal.  $M_2$  length (Fig. 1B;  $CV=3.72$ ) and  $P_3$  buccal height (Fig. 1F;  $CV=5.64$ ) are considered bimodal, though not with certainty.  $M_1$  length (Fig. 1A;  $CV=3.71$ ) may represent a bimodal distribution but could equally be a sample from a unimodal, normal distribution;  $P_3$  length (Fig. 1D;  $CV=4.00$ ) and  $P_3$  posterior width (Fig. 1E;  $CV=5.07$ ) distributions could each be described either as having 2 or 3 peaks, or as representing single normal distributions. Kolmogorov-Smirnov Lilliefors tests indicate that some of the univariate distributions differ significantly from normal (Table 2) and comparison with Table 1 shows that these include several with low variation. Thus univariate frequency distributions hint that the sample represents more than one population, but do not provide a basis for subdivision.

Bivariate plots (Fig. 2) suggest no clear divisions other than those evident in the univariate distributions, such as the apparent bimodality of  $M_2$  length (Fig. 1B, 2B). They show that specimens from Systems B and C have overlapping distributions, but that for some measurements, specimens from System C sites are, on average, smaller than specimens from System B sites. This is so for  $M_1$  length and  $P_3$  length (Fig. 2A, 2C) and to a lesser extent for  $M_2$  length (Fig. 2B).

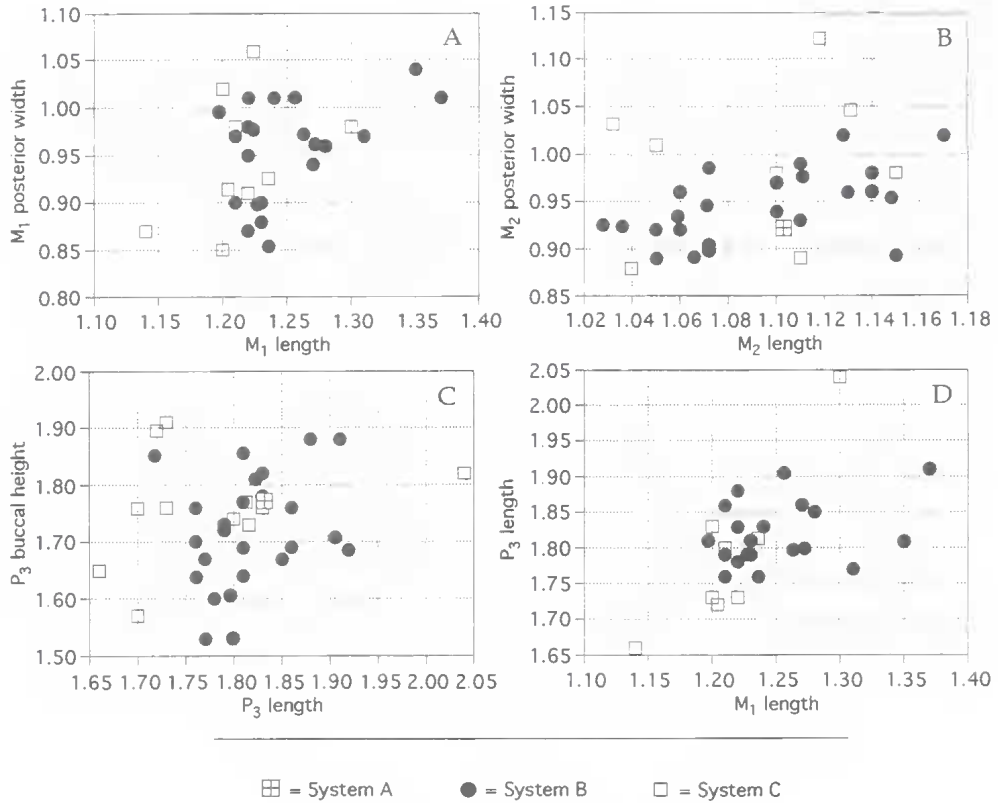


FIG. 2. Bivariate plots for some lower tooth measurements of Riversleigh *Burramys* specimens. All measurements inmm.

TABLE 2. Column 1, Kolmogorov-Smirnov Lilliefors tests for normality. Probability (P) values below 0.05 indicate a difference from normality significant at the 95% level. Columns 2 and 3, mean values for Systems B and C respectively. Column 4, Students t-tests; P indicates a significant difference between Systems B and C. Abbreviations as for Table 1.

	Lilliefors Test (P)	Mean - System B	Mean - System C	T-test (P)
P <sub>3</sub> L	0.088	1.82	1.79	0.266
P <sub>3</sub> AW	0.175	1.03	1.05	0.474
P <sub>3</sub> PW	0.455	1.22	1.22	0.928
P <sub>3</sub> MW	0.678	1.26	1.29	0.211
P <sub>3</sub> LH	0.215	1.43	1.44	0.923
P <sub>3</sub> BH	0.904	1.72	1.76	0.254
M <sub>1</sub> L	0.002	1.25	1.21	0.071
M <sub>1</sub> AW	0.193	0.79	0.76	0.268
M <sub>1</sub> PW	0.072	0.96	0.95	0.625
M <sub>2</sub> L	0.009	1.09	1.09	0.903
M <sub>2</sub> AW	0.009	0.87	0.91	0.041
M <sub>2</sub> PW	0.585	0.95	0.98	0.111
M <sub>3</sub> L	0.593	0.93	0.98	0.458
M <sub>3</sub> AW	0.177	0.85	0.81	0.394
M <sub>3</sub> PW	0.038	0.85	0.81	0.458
M <sub>1-2</sub>	0.054	2.32	2.27	0.226
M <sub>1-3</sub>	0.001	3.25	3.16	0.529

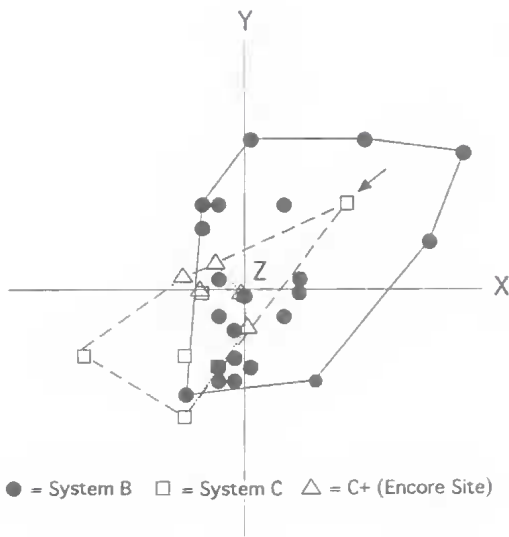


FIG. 3. Specimens of *Burramys* from various sites at Riversleigh plotted on principal component axes obtained using 11 measurements from P<sub>3</sub> and M<sub>1-2</sub>. Eigenvectors recorded in Table 3. X = first principal axis, Y = second principal axis, Z (perpendicular to page) = third principal axis. Solid line encloses specimens from System B sites. Dashed line encloses specimens from System C sites, including Encore Site. Dotted line encloses from System C 'aberrant' specimen QMF30104, indicated by arrow.

but appears not to be the case for P<sub>3</sub> buccal height (Figs 2C). M<sub>2</sub> posterior width shows the opposite trend (Fig. 2B), whereby System C specimens are on average larger than System B specimens. Student's t-tests show these differences to be non-significant at the 95% level (Table 2), but a principal components analysis employing dimensions of P<sub>3</sub> and M<sub>1-2</sub> (Fig. 3, Table 3) confirms

that total variation is explained partly by System C specimens being smaller than system B specimens. Eigenvectors for component 1 are all positive (Table 3), indicating that this is a general 'size component'; specimens scoring high on the first component (i.e. falling further towards the positive, or right-hand side of the X-axis in Fig. 3) are larger than those to the left. Although there is considerable overlap between Systems B and C, the centre of mass of the System B distribution is further to the right than that for System C.

Specimens from Encore site (younger than System C, ?early late Miocene) cluster at one extreme of the System C distribution, with the exception of a single large aberrant specimen QMF30104 from Gag Site (Fig.3). In the System B-System C continuum (Fig. 3) the cluster of Encore Site specimens falls on the 'older' (System B) end of the System C spectrum.

Despite the apparent trend of mean difference between specimens from Systems B and C, specimens from both Systems are present in each of the apparent peaks of the univariate distributions (Fig. 1A-F). This suggests that the underlying structure of the sample is not simply anagenetic change tracked from the older System B sites to younger System C sites, though such may have occurred. The bimodality of several of the frequency histograms may reflect sexual dimorphism and/or 2 roughly contemporaneous taxa. This suggestion is also supported by data plotted against sites arranged in estimated stratigraphic order (Fig. 4A-F.) Although samples from individual sites are inadequate to compare within- and between-site variation statistically, variation between sites is only a little greater than that within Upper site, provenance of the largest sample. Caution is therefore necessary when interpreting apparent between- or across-site trends (such

TABLE 3. Results of principal components analysis using 11 measurements of P<sub>3</sub> and M<sub>1-2</sub> of *Burramys* specimens from Riversleigh. Abbreviations as for Table 1.

Component	1	2	3	4	5	6	7	8	9	10	11
Eigen Value:	4.971	2.177	1.179	0.803	0.638	0.497	0.336	0.230	0.097	0.049	0.022
Percent	45.194	19.790	10.716	7.299	5.801	4.519	3.056	2.092	0.883	0.447	0.203
Cumulative percent:	45.194	64.984	75.699	82.998	88.799	93.318	96.374	98.466	99.350	99.797	100.000
Eigenvectors:											
M <sub>1</sub> L	0.304	-0.297	0.076	0.510	-0.328	0.126	0.172	-0.398	0.088	0.304	0.376
M <sub>1</sub> AW	0.323	-0.178	-0.285	0.040	0.397	-0.500	0.507	-0.020	-0.033	0.188	-0.282
M <sub>1</sub> PW	0.387	0.005	-0.265	-0.199	0.131	-0.356	-0.414	0.033	0.006	-0.188	0.623
M <sub>2</sub> L	0.209	-0.489	0.152	-0.278	0.293	0.353	-0.240	0.294	0.277	0.426	-0.060
M <sub>2</sub> AW	0.203	0.368	-0.472	-0.204	-0.053	0.535	0.381	0.193	-0.138	0.152	0.213
M <sub>2</sub> PW	0.362	0.150	-0.390	0.127	-0.107	0.168	-0.380	-0.299	0.338	-0.150	-0.518
M <sub>1-2</sub>	0.324	-0.403	0.142	-0.106	0.051	0.290	0.099	-0.117	-0.507	-0.567	-0.111
P <sub>3</sub> L	0.363	0.015	0.179	0.117	-0.512	-0.184	0.118	0.666	0.169	-0.164	-0.117
P <sub>3</sub> PW	0.188	0.344	0.215	0.617	0.510	0.146	-0.184	0.248	-0.204	0.018	0.016
P <sub>3</sub> LH	0.322	0.303	0.313	-0.303	-0.219	-0.159	-0.198	-0.191	-0.468	0.461	-0.187
P <sub>3</sub> BH	0.250	0.332	0.498	-0.258	0.211	0.056	0.313	-0.267	0.486	-0.218	0.112

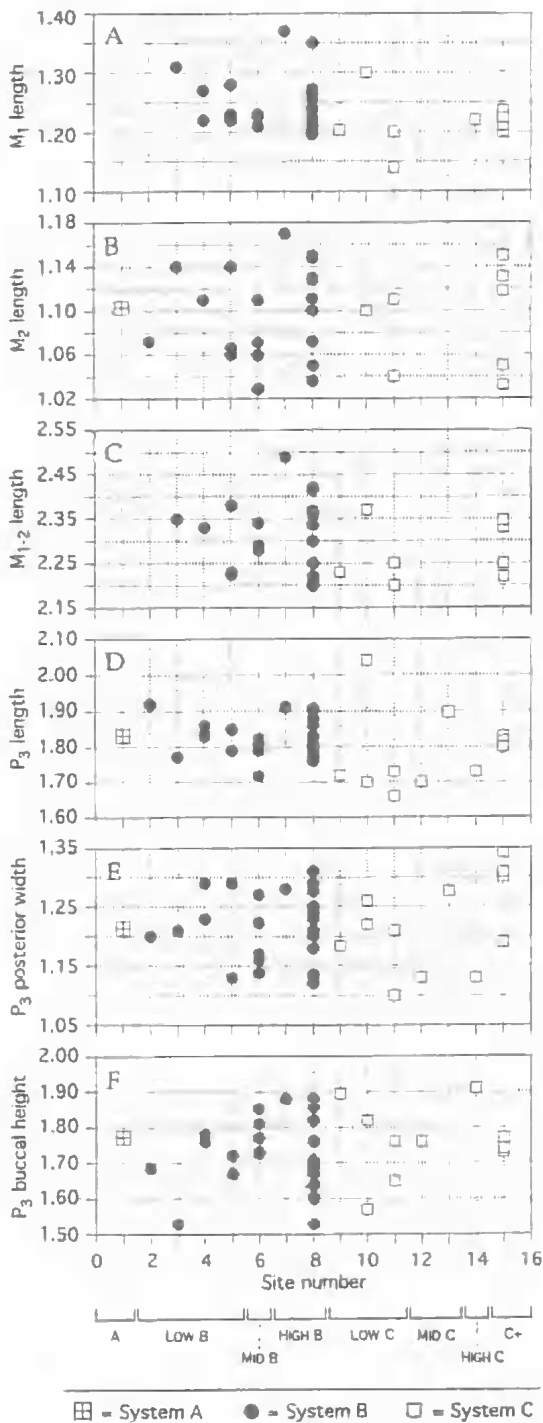


FIG. 4. Riversleigh *Berramys*: size measures against sites in stratigraphic sequence (Archer et al., 1989). Distances on horizontal axis arbitrary. Sites: 1=White Hunter; 2=Creaser's Ramparts; 3=Outasite; 4=RSO;

as size decline over time) as being significant. Although site 8 (Fig.4) includes Ten Bags Site, Mike's Potato Patch and Upper Site, most specimens are from Upper Site and these span the range of variation at site 8.

If two morphotypes are present they are both represented in Upper Site (Fig.4). Muirhead (1994) demonstrated size-guilding comparable to that in Recent mammal communities among 7 Upper Site bandicoot species separated on size; this is possibly due to competitive displacement of taxa that eat size-variable foods such as seeds or insects within a single community. Thus, Upper Site probably represents a single diverse community and the 2 morphotypes of *Berramys* could be sexual dimorphs or sympatric taxa. We reject sympatry because of morphological consistency of specimens falling near the peaks in the  $M_{1+2}$  length distribution; the size difference between those peaks is too small (Roth, 1981) to represent 2 species in different niches at the same level of a food web. The ratio of the second peak to the first (Fig. 1A-C) is 1.06, short of the oft-cited cutoff value of 1.3. (Roth (1981) showed that the 'constant ratio rule' is empirically unsubstantiated, but suggested that character displacement is unlikely to be indicated by ratio values lower than 1.3.)

Challenging the likelihood of either sexual dimorphism or sympatry is the fact that some specimens are in the higher peak of apparently bimodal distributions for some measurements, but the lower peak for others; whereas other specimens remain in one peak or the other for all or most measurements. There appears to be no combination of features that can be used to subdivide the sample; this is supported by the multivariate analysis (Fig. 3) which fails to divide the sample. A general trend to declining size through Systems B and C (Figs 2,3,4A,C) is evident, but some Encore Site specimens suggest reversal of the trend.

#### SUMMARY

Riversleigh *Berramys* specimens may represent two populations. Patterns of variation also suggest a cline of decreasing size through time; however, small sample sizes and uncertainty of relative ages limit the reliability of this observa-

5=Wayne's Wok; 6=Camel Sputum, Neville's Garden and Dirk's Towers; 7=Inabeyance; 8=Ten Bags, Mike's Potato Patch and Upper Site; 9=Kangaroo Jaw; 10=Gag; 11=Last Minute; 12=Main Site; 13= Jim's Jaw; 14=Wang; 15=Encore.

tion. If two populations have been sampled, magnitude and distribution of variation suggest that these are males and females of 1 species. Extant populations of *B. parvus* are not dentally dimorphic (Brammall, unpubl.), but their alpine habitat is far removed from the Miocene rainforest environment at Riversleigh (Archer et al., 1989, 1991) so it is not possible to infer that Recent and Miocene *Burramys* share population structures. We recognise a single new species.

#### SYSTEMATIC PALAEOLOGY

Class Mammalia Linnaeus, 1758  
 Supercohort Marsupialia Illiger, 1811  
 Order Diprotodontia Owen, 1866  
 Superfamily Burramyoidea Broom 1898  
 Family Burramyidae Broom, 1898

#### *Burramys* Broom, 1896

#### *Burramys brutyi* sp. nov. (Figs 5-9; Tables 1,4)

**ETYMOLOGY.** For the late Arthur Bruty who, together with his daughter Elaine Clarke, helped collect many specimens and discovered Bruty & the Beast Site on the Gag Plateau.

**MATERIAL.** Holotype QMF30102 (Fig. 5), a left dentary (DEN) with I<sub>1</sub>, P<sub>1-3</sub>, M<sub>1-2</sub> and alveoli for I<sub>2</sub> and M<sub>3-4</sub>. The tip of I<sub>1</sub> is missing, as are the condylar, angular and coronoid processes. Paratypes QMF30176 (Fig. 6), R DEN with P<sub>2-3</sub>, M<sub>1-4</sub>, broken anterior to P<sub>2</sub> and missing the ascending ramus and condylar, angular and coronoid processes, QMF30091 (Fig. 7), L maxilla with P<sup>2-3</sup>, M<sup>1-4</sup> and palate medial to cheekteeth. Types from early to mid-Miocene Upper Site on Godhelp Hill, DSite Plateau.

Other material: SYSTEM A - White Hunter Site, QMF23344, RM<sub>2</sub>; QMF23500, DEN with RP<sub>3</sub>, SYSTEM B - Camel Sputum Site, QMF20732, DEN with RM<sub>1</sub>, P<sub>3</sub>; QMF20735, R DEN; QMF20736, LM<sup>2</sup>; QMF30090, maxilla with LP<sup>2-3</sup>, M<sup>1</sup>; QMF30107, DEN with LI<sub>1</sub>, P<sub>2-3</sub>, M<sub>1-2</sub>; QMF30110, DEN with RI<sub>1</sub>, P<sub>2-3</sub>, M<sub>1-2</sub>. Inabeyance Site: QMF30079, DEN with LP<sub>3</sub>, M<sub>1-3</sub>; Mike's Potato Patch Site: QMF20759, DEN with LM<sub>2</sub>; QMF20760, LM<sup>1</sup>; QMF20761, P<sub>3</sub> or P<sup>3</sup>. Neville's Garden Site: QMF20718, DEN with RP<sub>3</sub>, M<sub>1</sub>; QMF20748, LM<sub>2</sub>; QMF20902, DEN with RI<sub>1</sub>, P<sub>3</sub>, M<sub>1</sub>; QMF23349, DEN with LP<sub>3</sub>, M<sub>1-2</sub>; QMF23376, DEN with RP<sub>3</sub>, M<sub>1</sub>; QMF23511, DEN with RP<sub>3</sub>; QMF24261, maxilla with RP<sup>2-3</sup>; QMF30089, maxilla with RP<sup>2-3</sup>, M<sup>1-2</sup>; QMF30092, maxilla with RP<sup>2-3</sup>, M<sup>1-4</sup>; QMF30113, DEN with RP<sub>3</sub>, M<sub>1</sub>; QMF30114, LP<sup>3</sup>; QMF30132, DEN with LP<sub>3</sub>, M<sub>1-2</sub>; QMF30271, RM<sup>3</sup>. Outasite: QMF20769, L DEN; QMF30080, DEN with LI<sub>1</sub>, P<sub>3</sub>, M<sub>1-3</sub>, RSO Site: QMF30081, DEN

with LP<sub>3</sub>, M<sub>1-3</sub>; QMF30084, DEN with RI<sub>1</sub>, P<sub>3</sub>, M<sub>1</sub>; QMF30094, maxilla with RP<sup>2</sup>; QMF30140, LP<sub>3</sub>; QMF30141, LP<sup>3</sup>; QMF30142, RP<sup>3</sup>. Ten Bags Site: QMF23502, DEN with LP<sub>3</sub>, M<sub>1</sub> Upper Site: QMF20774, DEN with RI<sub>1</sub>; QMF20775, DEN with LI<sub>1</sub>, P<sub>3</sub>; QMF20776, DEN with RP<sub>3</sub>; QMF20777, DEN with RM<sub>2</sub>; QMF20785, maxilla with RM<sup>1-3</sup>; QMF20786, DEN with LM<sub>1-3</sub>, P<sub>3</sub>; QMF20787, maxilla with LM<sup>1</sup>, P<sup>2-3</sup>; QMF20788, maxilla with LM<sup>1</sup>; QMF30082, DEN with LP<sub>3</sub>, M<sub>1-2</sub>; QMF30083, DEN with RP<sub>2-3</sub>, M<sub>1-2</sub>; QMF30085, DEN with LI<sub>1</sub>, P<sub>3</sub>, M<sub>1</sub>; QMF30086, DEN with RI<sub>1</sub>, P<sub>2-3</sub>, M<sub>1-2</sub>; QMF30087, maxilla with LP<sup>2-3</sup>; QMF30088, maxilla with LP<sup>2-3</sup>; QMF30091, maxilla with LP<sup>2-3</sup>, M<sup>1-4</sup>; QMF30095, maxilla with RP<sup>3</sup>, M<sup>1-2</sup>; QMF30096, maxilla with LP<sup>3</sup>; QMF30097, maxilla with RP<sup>3</sup>; QMF30098, maxilla with RP<sup>3</sup>, M<sup>1</sup>; QMF30099, maxilla with RP<sup>3</sup>; QMF30101, maxilla with LP<sup>2-3</sup>, M<sup>1-2</sup>; QMF30102, DEN with LI<sub>1</sub>, P<sub>1-3</sub>, M<sub>1-2</sub>; QMF30103, maxilla with LP<sup>3</sup>, M<sup>1</sup>; QMF30106, DEN with RI<sub>1</sub>, P<sub>2-3</sub>; QMF30111, DEN with LI<sub>1</sub>, P<sub>2-3</sub>, M<sub>1</sub>; QMF30112, DEN with RI<sub>1</sub>, P<sub>3</sub>; QMF30117, DEN with RP<sub>3</sub>, M<sub>1-2</sub>; QMF30118, DEN with RI<sub>1</sub>, P<sub>3</sub>, M<sub>1</sub>; QMF30119, DEN with RM<sub>2-3</sub>; QMF30120, DEN with LP<sub>3</sub>, M<sub>1-2</sub>; QMF30121, DEN with LI<sub>1</sub>, P<sub>3</sub>; QMF30122, DEN with LI<sub>1</sub>, P<sub>3</sub>; QMF30123, DEN with LP<sub>3</sub>, M<sub>1-2</sub>; QMF30124, DEN with RP<sub>3</sub>, M<sub>1-3</sub>; QMF30125, DEN with RP<sub>3</sub>, M<sub>1</sub>; QMF30127, DEN with LI<sub>1</sub>, P<sub>3</sub>; QMF30128, DEN with RP<sub>3</sub>; QMF30129, R DEN; QMF30130, 30131, L DEN; QMF30133, DEN with RP<sub>3</sub>, M<sub>1-2</sub>; QMF30138, maxilla with LP<sup>2</sup>; QMF30139, RP<sup>2</sup>; QMF30146, 30148, 30149, 30152 LP<sub>3</sub>; QMF30147, 30150, 30154, 30155, 30179, 30182 LP<sup>3</sup>; QMF30151, 30153, 30174, 30180, 30184 RP<sup>3</sup>; QMF30160, LM<sub>2</sub>; QMF30164-30167, LM<sup>1</sup>; QMF30168, 30173, 30177 RM<sup>1</sup>; QMF30176, DEN with RP<sub>2-3</sub>, M<sub>1-4</sub>; QMF30181, 30183 RP<sub>3</sub>; QMF30185, 30190 RM<sub>3</sub>; QMF30186, RM<sup>2</sup>; QMF30187, LI<sub>1</sub>; QMF30188, RI<sub>1</sub>; QMF30189, RM<sub>2</sub>. Wayne's Wok Site: QMF20725, maxilla with RP<sup>3</sup>; QMF20726, maxilla with RM<sup>1-2</sup>; QMF20737, maxillary fragment with RP<sup>3</sup>; QMF20738, DEN with RM<sub>1</sub>; QMF20744, DEN with RM<sub>1</sub>, P<sub>3</sub>; QMF20745, DEN with LM<sub>2-3</sub>; QMF20746, DEN with RM<sub>1-2</sub>; QMF22816, maxilla with RP<sup>2-3</sup>, M<sup>1-4</sup>; QMF30108, DEN with RP<sub>2-3</sub>, M<sub>1-2</sub>; QMF30136, DEN with LP<sub>3</sub>, M<sub>1</sub>. Wayne's Wok 2 Site: QMF30100, DEN with RI<sub>1</sub>, P<sub>3</sub>, M<sub>1-3</sub>; QMF30175, LP<sup>3</sup>. SYSTEM B OR C - Cleft of Ages 1 Site: QMF20905, R DEN, Cleft of Ages 2A Site: QMF22772, maxilla with RP<sup>3</sup>, M<sup>1</sup>. Cleft of Ages 4 Site: QMF20767, RP<sup>3</sup>; QMF20835, RP<sup>3</sup>; QMF20836, RP<sub>3</sub>; QMF23200, RP<sup>3</sup>. SYSTEM C - Encore Site: QMF20752, LM<sub>3</sub>; QMF20753, LP<sub>3</sub>; QMF20754, LM<sub>1</sub>; QMF20904, DEN with RM<sub>1-2</sub>, P<sub>2</sub>, 3; QMF23462, DEN with RM<sub>1-2</sub>, P<sub>3</sub>; QMF24334, DEN with LM<sub>1-2</sub>; QMF24424, DEN with LM<sub>1</sub>; QMF24426, DEN with LI<sub>1</sub>, P<sub>3</sub>, M<sub>2</sub>; QMF24552, RP<sup>3</sup>; QMF24727, DEN with LI<sub>1</sub>, P<sub>3</sub>, M<sub>1-2</sub>. Gag Site: QMF30078, DEN with RP<sub>3</sub>; QMF30093, maxilla with LP<sup>3</sup>; QMF30104, DEN with LI<sub>1</sub>, M<sub>1-2</sub>, P<sub>3</sub>; QMF30134, L DEN; QMF30135, DEN with LP<sub>3</sub>, M<sub>1</sub>

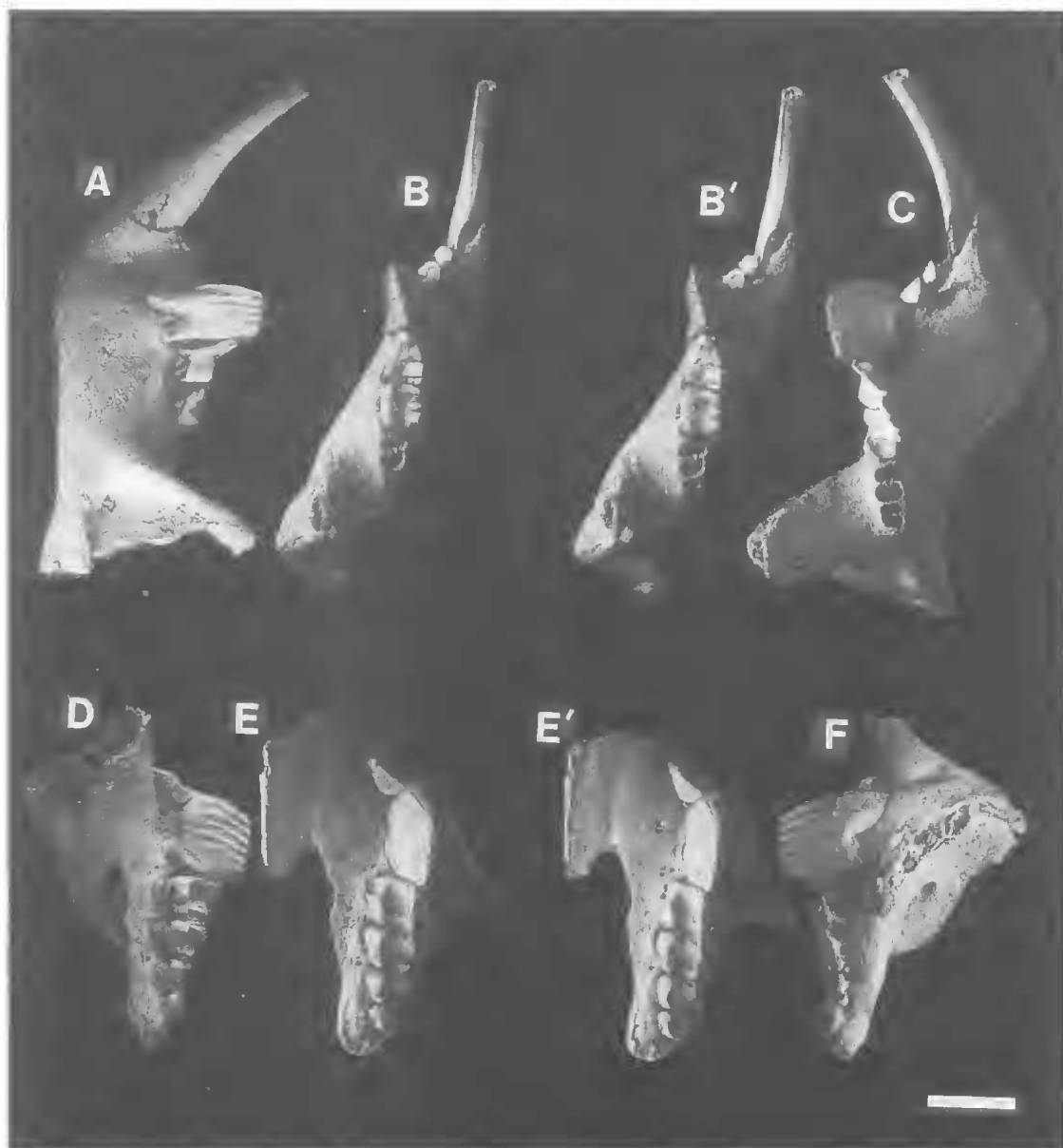


FIG. 5. A-C, *Burramys brutyi* n. sp. holotype QMF30102. Left dentary with I<sub>1</sub> P<sub>2-3</sub> M<sub>1-2</sub> in (A) buccal, (B-B') occlusal stereopair and (C) lingual views. D-F, *Burramys brutyi* paratype QMF30091. Left maxilla with P<sup>2-3</sup> M<sup>1-4</sup> in (D) buccal, (E-E') occlusal stereopair and (F) lingual views. Scale = 2mm.

QMF30137, LP<sup>3</sup>, QMF30156, LM<sub>2</sub>; QMF30157, RM<sup>1</sup>; QMF30158, RM<sub>1</sub>; QMF30161, LM<sup>3</sup>; QMF30170, RP<sup>3</sup>, QMF30171, RP<sub>3</sub>. Henk's Hollow Site: QMF30172, LP<sup>3</sup>. Jim's Jaw Site: QMF30178, DEN with RP<sub>3</sub>. Kangaroo Jaw Site: QMF30115, DEN with RP<sub>3</sub>, M<sub>1-2</sub>. Last Minute Site: QMF30105, DEN with R<sub>1</sub>, M<sub>1-3</sub>, P<sub>2-3</sub>; QMF30116, DEN with RP<sub>3</sub>, M<sub>1-2</sub>; QMF30143, LP<sup>3</sup>; QMF30144, RP<sub>3</sub>;

QMF30145, LP<sup>3</sup> apical fragment; QMF30162, RM<sup>3</sup>; QMF30163, RM<sup>3</sup>; QMF30169, DEN with RP<sub>3</sub>, M<sub>1</sub>. Main Site: QMF30109, DEN with RP<sub>3</sub>. Ringtail Site: QMF20756, RP<sup>3</sup>; QMF20757, maxilla with RM<sup>1-2</sup>, P<sup>3</sup>. Wang Site: QMF20763, maxilla with LP<sup>3</sup>; QMF20766, DEN with RM<sub>1</sub>, P<sub>3</sub>; QMF30272, RP<sub>3</sub>. AGE UNCERTAIN - Creaser's Ramparts Site: QMF20771, LP<sub>3</sub>.



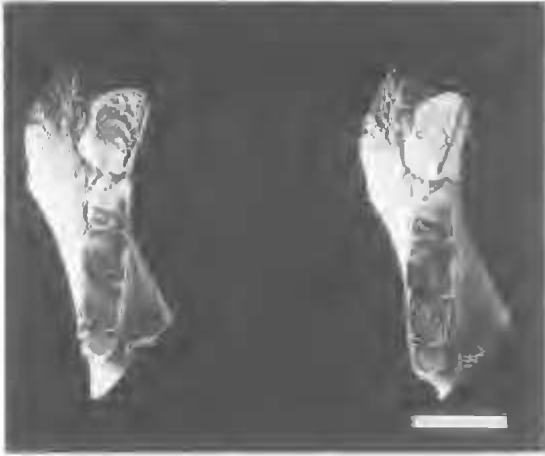


FIG. 6. *Burramys brutyi* paratype QMF30176: occlusal stereopair of right dentary fragment with P<sub>2-3</sub> and M<sub>1-4</sub>. Scale = 2mm.

**DIAGNOSIS.** Differs from *B. triradiatus* and *B. parvus* in being smaller, in having upper and lower plagiolacoid P<sub>3</sub> smaller and with fewer (5-6) cuspules and associated ridges and in having 2-rooted upper and lower M<sub>4</sub>. Dentary and maxilla more robust than in *B. parvus*, with smaller palatal vacuities, shorter I<sub>2</sub>-P<sub>2</sub> interval and less reduced posterior molars. P<sub>3</sub> with larger crown and larger posterior root than that of *B. wakefieldi* and diverging less from anteroposterior molar row axis. P<sub>1,2</sub> double-rooted; single-rooted in *B. wakefieldi*. Distinguishable from *B. wakefieldi* and *B. parvus* by M<sub>1</sub> cusp morphology: protoconid more lingual in *B. wakefieldi* than *B. parvus* or *B. brutyi*; metaconid more anterior in *B. parvus* than *B. brutyi* or *B. wakefieldi*.

**COMPARATIVE DESCRIPTION.** The dentary of *B. brutyi* is subequal to that of *B. wakefieldi* in size and shape. Both are more robust than that of *B. parvus* but slightly less so than that of *B. triradiatus*. The leading edge of the ascending ramus of *B. brutyi* is considerably more robust and rises at a steeper angle from the horizontal axis of the dentary than does that of *B. parvus*, but not quite as steeply as that of *B. triradiatus*. The I<sub>2</sub>-P<sub>2</sub> interval is shorter in *B. brutyi* than in *B. parvus* but is not as short, relative to the length of the ramus, as that of *B. triradiatus*.

Lower dentition. I<sub>1</sub> is long, slender and procumbent, with the tip curved upwards and slightly twisted. It is slightly less procumbent in *B. brutyi* than in *B. parvus*. The crown of I<sub>1</sub> is basally about the same dorsoventral thickness in *B. brutyi* and

*B. parvus* but a little thicker in *B. triradiatus*. I<sub>1</sub> of *B. brutyi* thins abruptly about half way along its exposed length, with the anterior half of the tooth being narrower than the posterior half. In lateral view I<sub>1</sub> of *B. brutyi* is more curved than in the other species.

I<sub>2</sub> has not been identified in *B. brutyi*, *B. wakefieldi* or *B. triradiatus*. In *B. parvus* I<sub>2</sub> is small and single-rooted, inserting into a shallow alveolus directly behind the posterior alveolar margin of I<sub>1</sub>. Its crown inclines forward to overlie I<sub>1</sub> posterobasally. In some specimens of *B. brutyi* there appears to be the remnant of a small alveolus in the fragile region between I<sub>1</sub> and P<sub>1</sub>, suggesting a small, single-rooted I<sub>2</sub>.

P<sub>1</sub> is small, 2-rooted and cap-like, the crown swelling beyond the roots in all directions. There is a minor ridge along the anteroposterior axis of the tooth, with the crown sloping away from the crest on each side towards the lingual and buccal margins respectively. In dorsal view it is almost circular in outline, being slightly wider than long. The crown does not extend as far beyond the roots posteriorly as it does in other directions. In *B. parvus* the crown is shorter and flatter than in *B. brutyi* and is also procumbent, rising slightly at its anterior end to overlie the posterior end of I<sub>2</sub>; it is ovoid in dorsal view (slightly longer anteroposteriorly) and its posterior end is reduced.

The anterior root of P<sub>1</sub> inserts anterobuccal to the posterior root. The posterior alveolus is closer to the anterior alveolus of P<sub>2</sub> than it is to the anterior alveolus of P<sub>1</sub>, inserting slightly lingually and anterior to the anterior alveolus of P<sub>2</sub>. The septum separating the posterior alveolus of P<sub>1</sub> and the anterior alveolus of P<sub>2</sub> frequently breaks down so that they form a single cavity. In some specimens, therefore, there may appear to be only three alveoli in the region which had been occupied by the 4 roots of P<sub>1</sub> and P<sub>2</sub>. Even with the septum intact, the arrangement of alveoli might suggest that the posterior alveolus of P<sub>1</sub> and the anterior alveolus of P<sub>2</sub> belonged to the same tooth. Whereas in *B. brutyi* the alveoli of P<sub>1</sub> and P<sub>2</sub> are closely but unevenly spaced, in *B. parvus* the 5 alveoli of I<sub>2</sub>, P<sub>1</sub> and P<sub>2</sub> are evenly spaced and in the adult animal there is a small gap between P<sub>1</sub> and P<sub>2</sub> (in subadult or younger animals the teeth are closer together).

P<sub>2</sub> is similar in shape but a little larger than P<sub>1</sub>. The slight anteroposterior crest lies at an angle (lingual posteriorly) across the alveolar margins, directly above an imaginary line joining the centres of the P<sub>2</sub> alveoli. Posteriorly the crown extends beyond and rises above the root,

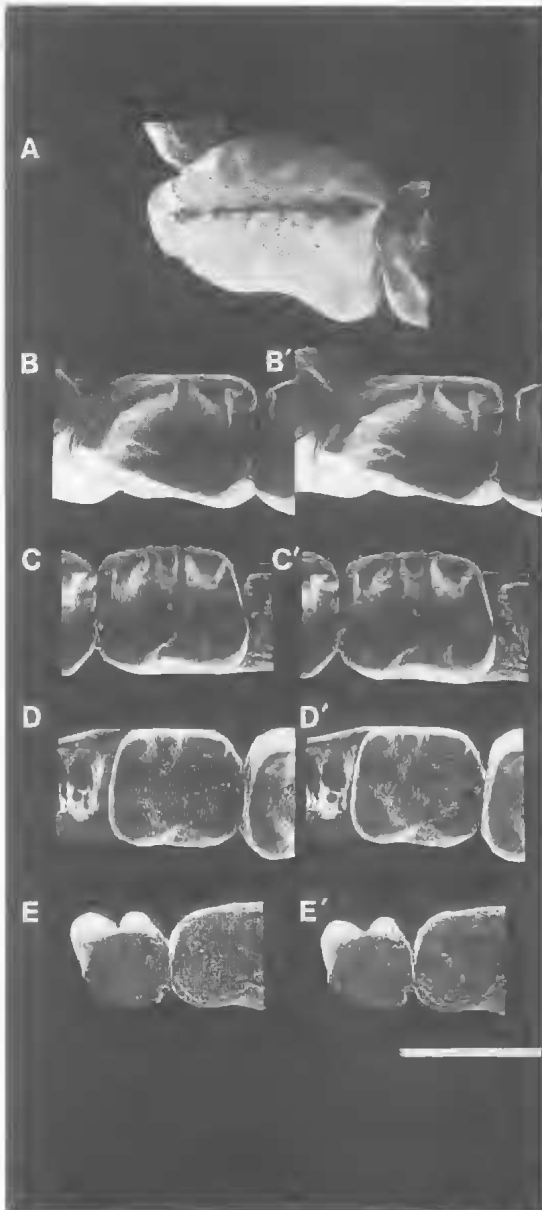


FIG. 7. Lower cheekteeth of *B. brutyi* in occlusal view. A-C, QMF 30102. A, LP<sub>3</sub>. B-B', LM<sub>1</sub>. C-C', LM<sub>2</sub>. D-D', RM<sub>3</sub> of QMF30100. E-E', RM<sub>4</sub> of QMF30176. B-E stereopairs. Scale = 1 mm.

terminating in a small cusplule and abutting P<sub>3</sub>. Anteriorly, the crown extends slightly beyond the root. Lingually and buccally the crown swells out and falls away to a rounded point on each side. The buccal, ventral apex is slightly higher and more anteriorly located than the lingual apex, so

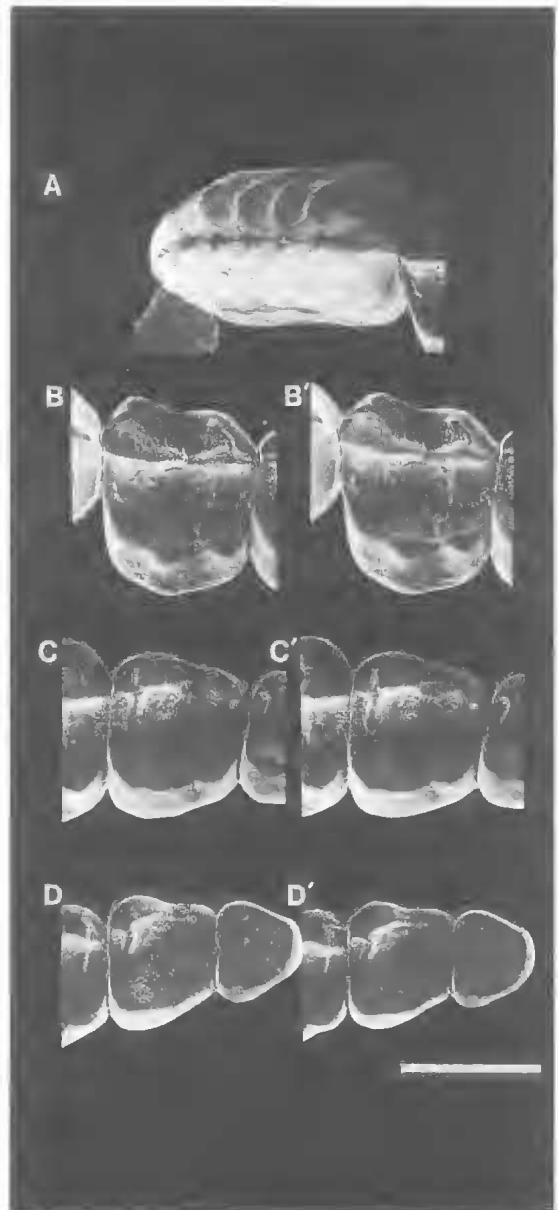


FIG. 8. Left upper cheekteeth of *B. brutyi* paratype QMF30091 in occlusal view. A, P<sub>3</sub>. B-B', M<sup>1</sup>. C-C', M<sup>2</sup>. D-D', M<sup>3-4</sup>. B-D stereopairs. Scale = 1 mm.

that the crown is somewhat twisted. In *B. parvus* P<sub>2</sub> is larger and relatively longer, with a crown that extends further beyond the roots, particularly anteriorly, giving the anterior end of the tooth a shelf-like appearance in lateral view. The crest is less clearly defined than in *B. brutyi* and approximately parallel to the axis of the I<sub>2</sub>-P<sub>2</sub> interval.

The crown of  $P_2$  shows less lingual-buccal asymmetry than in *B. brutyi*. The posterior end of the crown rises higher and more steeply than in *B. brutyi* with a distinct hump above the posterior root of the tooth, posterior to which the crown increases only slightly in height. The  $P_2$  of *B. triradiatus* is similar to, but larger than, that of *B. brutyi*. It is wider but shorter than  $P_2$  in *B. parvus* and almost circular in dorsal view. Although it protrudes beyond the roots in all directions, it is flatter than in *B. brutyi* and *B. parvus*. As with *B. brutyi*, the buccal side is displaced ahead of the lingual side and as with *B. parvus*, in lateral view the crown has an anterior 'lip'. The anteroposterior crest is poorly developed. A  $P_2$  (NMV P180016) assigned to *B. triradiatus* by Turnbull et al. (1987) is considerably larger than and different to  $P_2$  in the Holotype. It is 1-rooted, in contrast to  $P_2$  in the Holotype, which has 2 or 3 roots. NMV P180016 could possibly be a *B. triradiatus*  $P_2^2$ .  $P_2$  is not known from *B. wakefieldi* but appears to have been 1-rooted.

The plagiolacoid crown of  $P_3$  is longer and taller in *B. brutyi* than *B. wakefieldi*, larger in *B. parvus* and larger again in *B. triradiatus*.  $P_3$  of *B. brutyi* has 5 or 6 dorsal cusplules and associated ridges. The anterior edge of  $P_3$  rises vertically in *B. brutyi*, curving back dorsally to an almost horizontal serrated crest. The anterior profile is straight in *B. wakefieldi*, but leans backwards slightly as it rises to an also horizontal crest. The anterior root descends from the crown more anteriorly and buccally in *B. wakefieldi* than in *B. brutyi*. In *B. triradiatus* and *B. parvus*, the anterior profile of  $P_3$  curves forward then backward as it rises, giving the corrugated tooth a 'fanned' appearance and increasing the length of the dorsal edge. In *B. triradiatus* the anterior root curves forward slightly as it rises, with its convex profile continued by the crown. In *B. parvus* the root rises vertically to the base of the crown, then the crown expands gently forward. The  $P_3$  blade is slightly concave lingually and convex buccally. The exposed portion of the anterior root of  $P_3$  protrudes further beyond the jaw margin buccally in *B. brutyi* than in *B. parvus*. It is also in high relief in *B. wakefieldi* and *B. triradiatus*. In *B. parvus*, the posterior end of the crest has shifted lingually and backwards (relative to its position in *B. brutyi*). Thus the anterior angle between the long axis of the  $P_3$  crest and the molar row is greater in *B. parvus* than *B. brutyi*, as is the angle between this crest and its underlying roots. The posterior root of  $P_3$  is also smaller buccally in *B. parvus* than in *B. brutyi* and is smaller again in *B. wakefieldi*

because the posterior end of the crest and hence the direction of the bite force in that region has shifted lingually. The anterior end of  $P_3$  is more attenuated in *B. parvus* than in the other species. Some specimens of *B. brutyi* have cracks running from the dorsal cutting edge basally and backwards, stopping near the base of the crown.  $P_3$ s of each of the other species have similar cracks. They are particularly frequent and extensive in *B. triradiatus*. The  $P_3$ s of *B. triradiatus* also generally show more wear on the anterior end of the dorsal cutting edge than is evident in the other species.

Lower molars are bunodont in *Burramys*. They differ mainly in size,  $M_1$  cusp morphology and degree of reduction of  $M_4$ . Some unworn molars of *B. brutyi* are slightly crenulate, unlike other species of *Burramys*, but since crenulation is rare in *B. brutyi* and since molars of the other fossil species are poorly known, this feature is not regarded as diagnostic. The molar gradient is greater in *B. parvus* than in other species.

$M_1$  is approximately the same size in *B. brutyi* and *B. wakefieldi* and is larger in *B. parvus*. It has two roots in each of these species.  $M_1$  is not known from *B. triradiatus* but judging from its alveoli was 3-rooted and relatively small, with  $M_4 < M_1 < M_3 < M_2$ . The trigonid rises more steeply against  $P_3$  in *B. brutyi* and *B. wakefieldi* than in *B. parvus*, with the protoconid taller in comparison to the metaconid.  $P_3$  and  $M_1$  are therefore more disparate in height in *B. parvus* than in *B. brutyi* or *B. wakefieldi*. Posteriorly, the crown extends further beyond the roots in *B. parvus* than in the other species. In *B. wakefieldi* the entoconid is particularly tall. In all species, the  $M_1$  postmetaacristid is continuous with the longitudinal axis of the dorsal crest of  $P_3$ . In *B. brutyi* and *B. parvus* the premetaacristid swings buccally to meet the postmetaacristid, creating a disjunction between the  $P_3$  crest and the lingual crests of  $M_1$ . The postprotocristid/premetaacristid angle is more obtuse at the metaconid in *B. brutyi* than *B. parvus* because the metaconid is more posteriorly positioned in the former than the latter. The break in the  $P_3$ - $M_1$  blade system is therefore, longer in *B. brutyi* than in *B. parvus*. In *B. wakefieldi* the protoconid is more lingually positioned so that the crests associated with the  $P_3$  and  $M_1$  protoconid, metaconid and entoconid form an almost straight line.

$M_2$  is smaller in *B. brutyi* than *B. triradiatus* or *B. parvus*.  $M_2$  of the latter is slightly longer and narrower than that of *B. triradiatus*. It is proportionately shorter in *B. brutyi* than *B. parvus* and

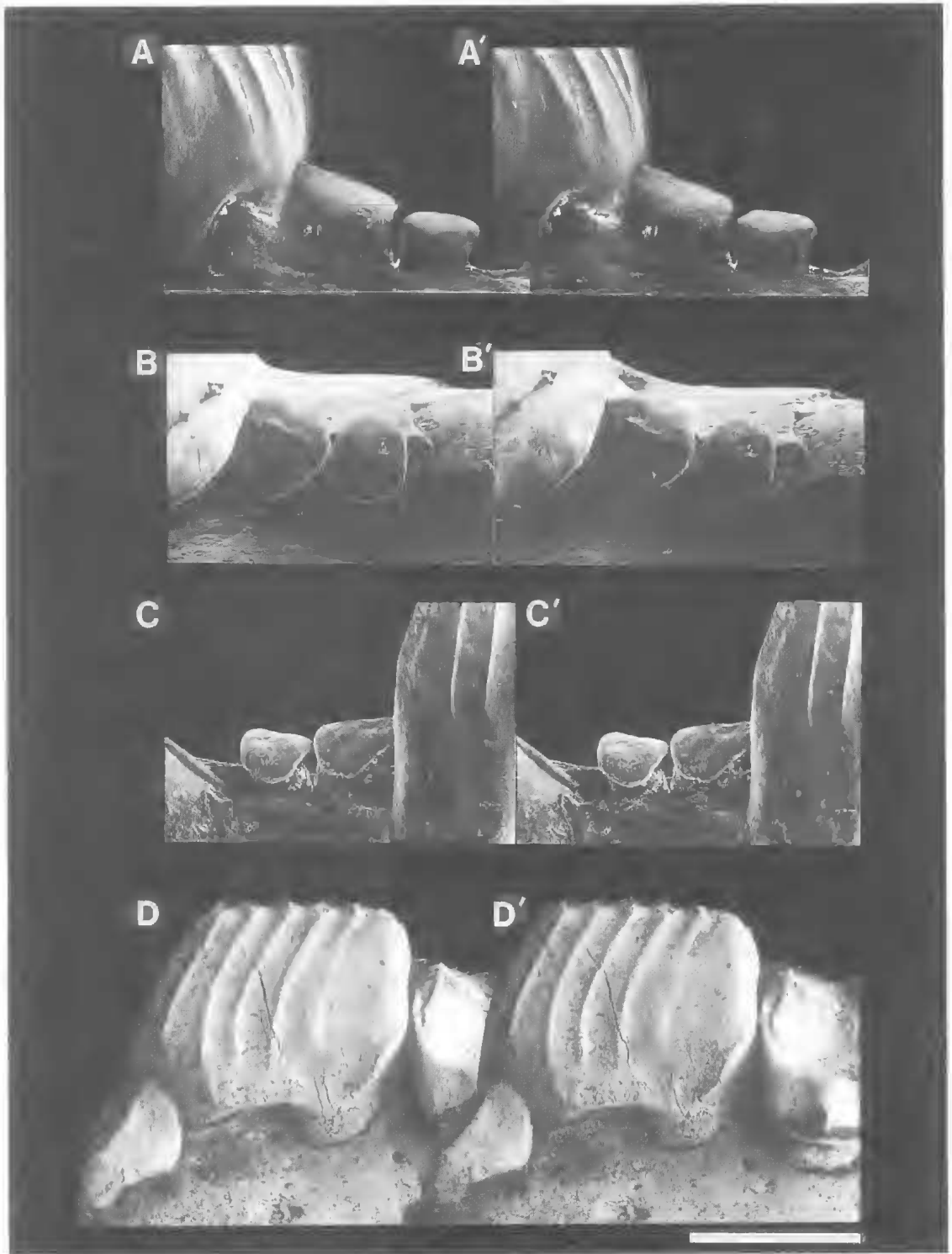


FIG. 9. *B. brutyi* sp. nov. A-C, left  $P_{1-2}$  with  $I_2$  alveolus and anterobasal portion of  $P_3$ , holotype QMF30102 in (A-A') lingual, (B-B') occlusal and (C-C') buccal views. D-D', left  $P_{2-3}$  and anterior portion of  $M^1$ , paratype QMF30091 in lingual view. A-D stereopairs. Scale = 1mm.

TABLE 4. Measurements of *B. brutyi* types. From holotype where possible. M<sub>3-4</sub> lengths and widths, M<sub>1-3</sub> and M<sub>1-4</sub> from paratype QMF30176. All upper tooth measurements from paratype QMF30176. Abbreviations as for Table 1.

Lower teeth		Upper teeth	
P <sub>1</sub> L	0.48	P <sup>2</sup> L	1.01
P <sub>1</sub> MW	0.55	P <sup>2</sup> MW	0.60
P <sub>2</sub> L	0.62	P <sup>3</sup> L	1.91
P <sub>2</sub> MW	0.64	P <sup>3</sup> AW	0.92
P <sub>3</sub> L	1.76	P <sup>3</sup> PW	1.21
P <sub>3</sub> AW	1.07	P <sup>3</sup> MW	1.21
P <sub>3</sub> PW	1.23	P <sup>3</sup> LH	1.56
P <sub>3</sub> MW	1.31	P <sup>3</sup> BH	1.64
P <sub>3</sub> LH	1.45	M <sup>1</sup> L	1.11
P <sub>3</sub> BH	1.76	M <sup>1</sup> AW	1.17
M <sub>1</sub> L	1.21	M <sup>1</sup> PW	1.21
M <sub>1</sub> AW	0.83	M <sup>1</sup> MW	1.39
M <sub>1</sub> PW	0.97	M <sup>2</sup> L	0.96
M <sub>2</sub> L	1.10	M <sup>2</sup> AW	1.13
M <sub>2</sub> AW	0.88	M <sup>2</sup> PW	0.89
M <sub>2</sub> PW	0.94	M <sup>3</sup> L	0.82
M <sub>3</sub> L	0.98	M <sup>3</sup> AW	0.90
M <sub>3</sub> AW	0.85	M <sup>3</sup> PW	0.66
M <sub>3</sub> PW	0.80	M <sup>4</sup> L	0.64
M <sub>4</sub> L	0.66	M <sup>4</sup> AW	0.67
M <sub>4</sub> AW	0.64	M <sup>4</sup> PW	0.40
M <sub>4</sub> PW	0.50	M <sup>1-2</sup>	2.07
M <sub>1-2</sub>	2.30	M <sup>1-3</sup>	2.90
M <sub>1-3</sub>	3.18	M <sup>1-4</sup>	3.51
M <sub>1-4</sub>	3.83		

very slightly shorter than *B. triradiatus*. M<sub>2</sub> is not known for *B. wakefieldi*. It has two roots in each species except for *B. triradiatus*, in which it has three. In a few (<5%) of *B. brutyi* specimens the anterior alveolus has, ventrally, a septum (or remainder thereof) subdividing it basally into 2 compartments, suggesting a root bifurcated at its tip. This condition may be intermediate between the 2- and 3-rooted conditions. In *B. brutyi* and *B. parvus* there is frequently a small cuspid halfway along the lingual margin of the crown, at the junction of the postmetacristid and the pre-entocristid. Sometimes the cuspid is not clearly differentiated from the postprotocristid. It is the same size in both species even though the tooth is larger in *B. parvus*. The cuspid is not evident in *B. triradiatus*, although there is a small dorsal protuberance on the anterior end of the pre-entocristid of NMV P158628. In each species the postprotocristid curves lingually from the protoconid before straightening and running approximately parallel to the tooth axis until interrupted by the transverse hypoconid-entoconid lophid. Postprotocristid curvature is less extreme in *B.*

*brutyi* than the other species. The cristid obliqua lies parallel to the tooth axis, forming a posterobuccal cingular pocket between itself and the postprotocristid. In all species the buccal cusps are bulbous. The hypoconid causes the posterobuccal corner of the tooth to extend beyond its basically rectangular outline. The lingual cusps are slightly ahead of the buccal cusps, skewing the sides of the tooth slightly. They are more crescentic than the buccal cusps and, together with their associated crests, form a blade-like structure.

M<sub>3</sub> is similar to, but smaller than, M<sub>2</sub>. Cusps are lower and basins shallower, with the crown surface showing more wear than M<sub>2</sub>. M<sub>3</sub> is smaller in *B. brutyi* than the other species, is slightly larger in *B. triradiatus* than *B. parvus* and is not known from *B. wakefieldi*. Interspecific comparisons of M<sub>3</sub> are as for M<sub>2</sub> except that in *B. brutyi* and *B. parvus*, but not *B. triradiatus*, the lingual-buccal skew is slightly more pronounced than in M<sub>2</sub>. In all species M<sub>3</sub> is slightly shorter anteroposteriorly than M<sub>2</sub>. In *B. triradiatus* the protoconid and hypoconid of M<sub>3</sub> are subequal whereas in M<sub>2</sub> the hypoconid is larger. In M<sub>3</sub> there is a distinct cleft dividing the rounded protoconid and hypoconid.

M<sub>4</sub> in *B. brutyi* and *B. wakefieldi* has 2 roots, whereas in *B. triradiatus* it has 3 and in *B. parvus* 1. While most specimens of *B. brutyi* have 2 roots or alveoli for M<sub>4</sub>, some have 3 and a few had 1 root. Such variation is not evident in the *B. triradiatus* or *B. parvus*. M<sub>4</sub> is not known for *B. wakefieldi* or *B. triradiatus* but the alveoli of *B. triradiatus* suggest that it was far less reduced than in *B. parvus* and possibly less reduced than in *B. brutyi*. M<sub>4</sub> is low-crowned, with low cusps which quickly wear down. It is smallest and most degenerate in *B. parvus*.

Upper teeth of *Burramys* anterior to P<sup>2</sup> have not been recognised from Riversleigh or Hamilton, so discussion of the upper dentition will be limited to P<sup>2-3</sup> and M<sup>1-4</sup>. Skull fragments and upper teeth of *B. wakefieldi* are unknown. The upper dentition of *B. triradiatus* is known only from isolated teeth.

Maxilla. Palatal vacuities are smaller in *B. brutyi* than *B. parvus*. The anteroventral opening of the infraorbital foramen is also smaller (and less round) in *B. brutyi*, as are foramina in the alisphenoid and squamosal. Known bones of the skull are more robust in *B. brutyi* than in *B. parvus*. In both species the maxilla is swollen around the P<sup>3</sup> alveolus, between the lachrymal

and the infraorbital foramen. This swelling is more extensive in *B. parvus* than *B. brutyi*, with  $P^3$  and the anterior limit of the molar row beginning further forward in the living species. In ventral view, the anteromedial limit of the zygomatic arch in *B. brutyi* is level with a point midway between the protocone and protoconule of  $M^1$ . In *B. parvus* it is midway between the metaconule and protocone of  $M^1$ . The upper molar gradient is steeper in *B. parvus* than in the other species. In *B. brutyi* the molar row rotates buccally around the maxilla from front to back, to a greater degree than occurs in *B. parvus*.

Upper dentition.  $P^2$  of *B. brutyi* is 2-rooted and similar to, although slightly larger than,  $P_2$ . A weak crest runs from a small cuspule at the highest point on the crown, which is midway along the raised posterior edge, to the anterior base of the crown. Lingually and buccally the crown slopes towards the roots. The base of the crown expands lingually over the posterior root, extending the crown outline posterolingually. This swelling is less pronounced in *B. parvus*. In crown view the tooth is teardrop-shaped, being just wider than the transverse diameter of the anterior root. In *B. parvus*, by contrast, the 2-rooted  $P^2$  crown expands beyond the roots for its whole length (more so posteriorly than anteriorly). In both species the crown is parallel to the edge of the medially inclined palate, forming an angle with  $P^3$  and the molar row. Although  $P^2$  for *B. triradiatus* has not been identified, the small, single-rooted tooth (NMV P180016), determined by Turnbull et al. (1987) to be a  $P_2$ , is similar to  $P^2$ s of *B. brutyi* and *B. parvus* and is interpreted here to be  $P^2$ .

In *B. brutyi*, as in *B. triradiatus* and *B. parvus*,  $P^3$  is similar to  $P_3$ . Regarding  $P^3$  anteroposterior length, *B. brutyi* < *B. parvus* < *B. triradiatus*.  $P^3$  is dorsoventrally shortest in *B. brutyi* and slightly taller in *B. triradiatus* than *B. parvus*. It is similarly shaped in all three species but in *B. brutyi* the crown decreases in anteroposterior length from base to occlusal edge, whereas in *B. parvus* and *B. triradiatus* the ventral edge of the blade is at least as long as base of the crown. In anterior view,  $P^3$  of *B. brutyi* is as wide as that of *B. parvus* at its base, but tapers more rapidly and is hence thicker at the occlusal edge and more robust in appearance. In *B. triradiatus* the tooth is thicker basally than in *B. parvus* because of a broader cingulum (see below). It is thicker for most of its height but tapers to almost as thin an edge as does *B. parvus*  $P^3$ . Whereas the dentary turns medially

immediately anterior to  $P_3$ , the maxilla of *Burramys* turns medially only anterior to  $P^2$ .  $P^3$  therefore does not appear to turn out from the molar row as much as  $P_3$ ; its crest is approximately parallel to the molar row. Consequently it does not have to retract anterobasally (as with  $P_3$ ) to insert into the bone and unlike  $P_3$  its anterior edge, seen in lateral view, may appear to extend slightly forward basally. Probably as a consequence of this, the buccal-convexity/lingual-concavity is, in all species, less pronounced than in  $P_3$ . In occlusal view,  $P^3$  of *B. brutyi* is basically rectangular, but with the anterior end curving to a rounded point and the posterior corners rounded. In *B. parvus* and *B. triradiatus* it is more ovoid, the anterior end again being a little narrower than the posterior end, and pointed. There is a narrow cingulum, poorly developed at the anterior end, along the lingual and buccal sides of the crown. The cingulum is very weak in *B. brutyi*, slightly better developed in *B. parvus* and significantly better developed in *B. triradiatus*. In this species the cingulum is sometimes emphasised lingually by a vertical wear facet that terminates abruptly at the cingulum. In *B. triradiatus* and to some extent in *B. parvus* the second and sometimes third lingual ridges merge into the first which forms a curb that arcs back toward the cingulum. This curb is less prominent in *B. brutyi*, in which ridges approach the cingulum without merging.

In all species  $M^1$  has 3 roots — a larger lingual and 2 smaller buccal roots. In *B. brutyi*  $M^1$  is wider than it is long. In *B. parvus* and *B. triradiatus* it is about as wide as long. In all 3 species there is a swelling anterobuccal to the paracone such that the anterobuccal corner of the tooth is a little larger than the posterobuccal corner. In *B. brutyi* there is a distinct buccal cingular basin or shell at the intersection of the post-paraecrista and the premetaecrista extending back to the level of the metacone and forward nearly as far as the paracone. It is sometimes delimited anteriorly by a small crest running buccally from the paracone. In *B. parvus* this pocket is little more than a sloping cingular shelf. In *B. triradiatus* it is a narrow cingulum following the rounded paracone and metacone buccally (Turnbull et al., 1987, fig. 5A). The ectoloph of *B. brutyi* is roughly parallel to the anteroposterior axis of the tooth. As with *B. parvus*, the paracone is significantly larger than the other cusps, retaining its height as the tooth wears. The protoconule and metaconule are less developed in *B. brutyi* and *B. triradiatus* than in *B. parvus*. Hence in

occlusal view,  $M^1$  of *B. brutyi* is basically rectangular, with the anterior and posterior ends of the tooth parallel. In *B. parvus* it is longer and more curved lingually than buccally because of the inflated protoconule and metaconule. In occlusal view there is an indentation between the paracone and metacone in *B. brutyi* and *B. triradiatus*, whereas in *B. parvus* the crown outline between those cusps is almost straight.

$M^2$  is rectangular in *B. brutyi* (shorter anteroposteriorly) and considerably smaller than in either *B. triradiatus* or *B. parvus*, in both of which it is about as wide as it is long. In all species it has 3 roots and a small cingular pocket anterobuccal to the paracone, bounded lingually by a short preparacrista that runs perpendicularly from the anterior edge of the tooth to the paracone. The buccal cusps and their associated crests are blade-like in comparison to the more rounded lingual cusps. In *B. triradiatus* the buccal cusps are more pointed and the lingual cusps more rounded than in *B. brutyi* or *B. parvus*. The transverse lophs are also taller and consequently the cingular and central basins deeper. The protocone and metaconule are more approximated than in other species, as are the paracone and metacone. In unworn specimens of *B. parvus* the relative cusp heights are as reported for *B. triradiatus* (Turnbull et al. 1987): protocone exceeds metaconule while paracone is subequal to the metacone. In worn  $M^2$ s of *B. parvus* the lingual cusps are lower so that the paracone exceeds the metacone which exceeds the protocone which is subequal to the metaconule. This pattern of cusp wear appears to be the same in *B. brutyi*.

$M^3$  of *B. brutyi* is similar to  $M^2$  but is smaller, proportionately a little narrower (because the lingual cusps are less bulbous) and with cusps a little lower. The posterior cusps are more reduced than the anterior cusps and the metacone, in particular, is relatively lower. The metaconule is slightly further forward than in  $M^2$  so that the posterolingual corner of the tooth is more rounded in occlusal view. This feature is similar to the condition in *B. triradiatus* and, even more so, to the condition in *B. parvus*. The transverse lophs, pre- and post-cingula and their associated basins soon wear down to the level of the central basin.  $M^3$  is most reduced posteriorly in *B. parvus* and least reduced in *B. triradiatus*.

$M^4$  is larger, both relative to other molars and absolutely, in *B. brutyi* than in *B. parvus* and is also less posteriorly reduced. The posterior cusps, especially the metaconule, are markedly reduced. The anterior cusps, although low and rapidly

worn, are distinct in unworn teeth and remain distinguishable until late wear stages. Although the cusps, their associated crests and basins are low and quickly levelled, worn  $M^4$ s of *B. brutyi* shows more surface morphology than those of *B. parvus*, in which even newly-erupted  $M^4$ s are almost featureless.  $M^4$  has 3 roots in *B. brutyi*. Ride (1956) reports a double-rooted  $M^4$  in *B. parvus* but it appears from the specimens examined that the basic condition in *B. parvus* is a 3-rooted  $M^4$ , perhaps with a reduced number of roots in some specimens.

#### INTRAGENERIC PHYLOGENETIC ANALYSIS

Thirty-five characters were investigated for their potential to contribute to an analysis of the relationships between species of *Burramys*. *Cercartetus nanus*, *C. lepidus*, *C. caudatus* and *C. concinnus* were used as the primary outgroup since *Burramys* and *Cercartetus* are sister groups (Archer, 1984; Aplin & Archer, 1987). *Trichosurus caninus*, *T. arnhemensis*, *T. vulpecula*, *Spilococus maculatus* and *Phalanger carmelitae* were used as a secondary outgroup because DNA hybridisation indicates that burramyids and phalangerids are sister groups (Springer & Kirsch, 1989). Character numbers refer to Table 5; unnumbered characters are not included in the analysis.

1. Body size. Jaw lengths suggest that *B. brutyi* and *B. wakefieldi* were of similar body size. *B. triradiatus* and *B. parvus* are larger and approximately the same size as each other. *Cercartetus lepidus*, the smallest of its genus, is also regarded as the most primitive (Archer, 1984). Phalangerids are larger than burramyids but this is likely to be a derived condition; diverse taxa exhibit a general tendency for increasing body size over time (Maurer et al., 1992). The small size of *C. lepidus* suggests that larger size is apomorphic within *Burramys*. In our discussion of character states, a morphological feature is regarded as large only if its greater size is independent of increased body size.

2. Robustness. The dentary and maxilla of *B. parvus* are more slender than those of other *Burramys*, despite being larger. All species of *Cercartetus* have similarly slender jaws. *Trichosurus*, *Spilococus* and *Phalanger* are more robust than *Cercartetus* or *B. parvus*, but being several times larger than burramyids, they do not form a useful comparison in this regard. The slenderness of *Cercartetus* suggests that increased robustness is apomorphic in burramyids.

3. Length of I<sub>2</sub>-P<sub>2</sub> interval. The interval occupied by I<sub>2</sub>, P<sub>1</sub> and P<sub>2</sub> is longer relative to jaw length in *B. parvus*

TABLE 5. Characters and character polarities for intrageneric phylogenetic analysis of *Burramys* species. Plesiomorphic state denoted by 0; ? indicates that information on character is unavailable. A and B indicate alternative derived states.

Character	<i>B. brutyi</i>	<i>B. wakefieldi</i>	<i>B. triradiatus</i>	<i>B. parvus</i>
1 Body size	0	0	1	1
2 Robusticity	1	1	1	0
3 Length of I <sub>2</sub> -P <sub>2</sub> interval	1	1	2	0
4 Length of I <sub>1</sub>	0	?	2	1
5 Basal thickening of I <sub>1</sub>	1	?	1	0
6 Number of roots P <sub>1-2</sub>	0	1A	1B	0
7 Arrangement of alveoli P <sub>1-2</sub>	1	?	?	0
8 Size of P <sub>3</sub>	1	1	2	1
9 Size disparity between P <sub>3</sub> roots	1	3	2	2
10 Number of ridges P <sub>3</sub>	1	1	3	2
11 Curvature of P <sub>3</sub> anterior profile	0	0	1	1
12 Concave/convex P <sub>3</sub>	0	0	1	1
13 Arched dorsal edge P <sub>3</sub>	0	0	1	2
14 Divergence of P <sub>3</sub> from molar row	1	3	2	2
15 Transverse compression P <sub>3</sub>	1	1	3	2
16 Distinct M <sub>1</sub> talonid and trigonid	1	0	?	1
17 M <sub>1</sub> protoconid position	0	1	?	0
18 M <sub>1</sub> metaconid position	0	0	?	1
19 Relative length lower molars	2	2	1	0
20 Neomorphic cuspid	1	?	0	1
21 Loph(id) development M <sub>2-3</sub> , M <sup>2-3</sup>	1	?	0	1
22 No. roots M <sub>1-3</sub>	0	0	1	0
23 No. roots M <sub>4</sub>	0	0	1A	1B
24 Reduction of M <sub>4</sub>	1	1	0	2
25 Size of maxillary vacuities	0	?	?	1
26 Anterior limit P <sup>3</sup>	1	?	?	0
27 Rotation of upper molar row	1	?	?	0
28 Inflation of lingual cusps M <sup>1</sup>	0	?	0	1
29 Lingual displacement of M <sup>1</sup> paracone	0	?	0	1

than in *B. brutyi* or *B. triradiatus*, with *B. triradiatus* the shortest. This region is incomplete in the holotype of *B. wakefieldi* but appears to be about the same length as in *B. brutyi*. This interval is relatively long in *Cercartetus* and phalangerids, indicating that this is the plesiomorphic state.

4. I<sub>1</sub> length. I<sub>1</sub> is longer in *B. parvus* than *B. brutyi* and longer again in *B. triradiatus* (unknown in *B. wakefieldi*). It is shorter in *Cercartetus* than *Burramys* and is shorter in phalangerids. A long I<sub>1</sub> is regarded as apomorphic.

5. Thickened base of I<sub>1</sub>. In *B. brutyi* and *B. triradiatus* I<sub>1</sub> is thick basally (thicker in *B. triradiatus*) and immediately begins to taper; approximately half way along the exposed portion of the tooth it thins markedly then attenuates to the tip. In *B. parvus* I<sub>1</sub> tapers gradually without marked reduction at a particular point. In *Cercartetus*, *Trichosurus*, *Spilocuscus* and *Phalanger* I<sub>1</sub> does not change suddenly in diameter, suggesting that a basally thickened I<sub>1</sub> is apomorphic.

Shape of P<sub>1</sub>. P<sub>1</sub> is not known for *B. wakefieldi* or *B.*

*triradiatus*. In *B. brutyi* it is small, rounded and similar to P<sub>2</sub>. In *B. parvus* P<sub>1</sub> is intermediate between the cap-like P<sub>2</sub> and the slightly elongate, procumbent I<sub>2</sub>. In *C. caudatus* and *C. lepidus* P<sub>1</sub> and P<sub>2</sub> are both button-like and upright; in *C. uamus* and *C. concinnus* P<sub>1</sub> resembles I<sub>2</sub> almost as much as P<sub>2</sub>. *Trichosurus* and *Phalanger* species have extensive diastemata, lacking P<sub>1</sub> and P<sub>2</sub> analogous to those of burramyids. It is therefore unclear which state of P<sub>1</sub> is more plesiomorphic and although this character may be phylogenetically significant, a satisfactory polarity assignment cannot be made.

6. Number of roots P<sub>1</sub> and P<sub>2</sub>. *Burramys brutyi* and *B. parvus* have double-rooted P<sub>1</sub> and P<sub>2</sub>. *Burramys triradiatus* has a triple-rooted P<sub>2</sub> and double- or triple-rooted P<sub>1</sub>; the number of roots is not clear due to damage in the available material. P<sub>1</sub> and P<sub>2</sub> each appear to have been single-rooted in *B. wakefieldi*. P<sub>1</sub>-P<sub>2</sub> of *Cercartetus* possess sometimes one and sometimes two roots. P<sub>1</sub>-P<sub>2</sub> of *Trichosurus* and *Phalanger* are either extremely reduced or absent. Outgroup analysis does not resolve the polarity of this character. The normal marsupial premolar condition is two-rooted so this is



taken to be the plesiomorphic condition. *Burramys wakefieldi* and *B. triradiatus* are interpreted as having alternative derived states.

7. Arrangement of P<sub>1-2</sub> alveoli. In *B. parvus* the alveoli of P<sub>1-2</sub> are in a straight line between I<sub>2</sub> and P<sub>3</sub>. In *B. brutyi* the anterior alveolus of P<sub>2</sub> is lingual to its posterior alveolus and the posterior alveolus of P<sub>1</sub> is lingual to its anterior alveolus. *B. wakefieldi* and *B. triradiatus* have different numbers of roots for P<sub>1-2</sub> from *B. brutyi* and *B. parvus*, so their alveoli are not all homologous. In all species of *Cercartetus* the alveoli of P<sub>1-2</sub> lie in a straight line; this is also the case for *Trichosurus*, *Spilocuscus* and *Phalanger* (where the teeth occur). Linearly-arranged alveoli are therefore thought to be plesiomorphic for burramyids.

8. Size of plagiulacoid premolar. The sectorial premolar of *Cercartetus* and phalangerids (and M<sub>1</sub> of *C. concinnus*) is smaller than that of *Burramys*. It is therefore assumed that an enlarged plagiulacoid premolar is synapomorphic for *Burramys* and apomorphic within the genus. Although P<sub>3</sub> of *B. parvus* is larger than that of *B. wakefieldi* or *B. brutyi*, log-scaled plots of P<sub>3</sub> buccal crown surface area against jaw length (unpubl. data) suggest that P<sub>3</sub> of *B. parvus* is not disproportionately large for its body size. P<sub>3</sub> of *B. triradiatus*, on the other hand, departs significantly from the line of best fit for P<sub>3</sub> size against body size, being disproportionately large. P<sub>3</sub> of *B. wakefieldi* falls below the line, suggesting that it is disproportionately small, but Studentized residuals do not show its departure from the line to be significant.

9. Relative sizes of anterior and posterior roots of plagiulacoid premolar. Buccally, the posterior root of P<sub>3</sub> is smaller, relative to its anterior root and crown, in *B. wakefieldi* than in other *Burramys*. The posterior root of P<sub>3</sub> is smaller (relative to the anterior root and the crown) in *B. parvus* than in *B. brutyi*. The anterior root of the large P<sub>3</sub> of *B. triradiatus* is massive; although the posterior root is comparatively small, the disparity is not as great as that in *B. wakefieldi*. In *Cercartetus* and phalangerids, the anterior and posterior roots of the sectorial premolar are subequal; this is thought to be the plesiomorphic condition.

10. Number of ridges on plagiulacoid premolar. In *B. brutyi* and *B. wakefieldi* there are 5 or 6 ridges on each of the buccal and lingual faces of P<sub>3</sub> and 5 or 6 associated dorsal cuspules. The lack of posterior and weakness of anterior cuspules in the holotype of *B. wakefieldi* appears to be the result of extreme wear on the formerly serrated tooth. In *B. parvus* there are commonly 7 ridges and cuspules and in *B. triradiatus*. 9. Phalangerids with smaller, unridged P<sub>3</sub>s are thought to be more plesiomorphic than those with larger, ridged P<sub>3</sub>s (Flannery et al., 1987); all have fewer ridges and cuspules than *Burramys*. *Cercartetus nanus* and *C. caudatus* have a single sharp dorsal cusp on the sectorial premolar and *C. concinnus* one main cusp on its premolariform M<sub>1</sub>. A larger number of ridges and

cuspules is regarded as more derived within *Burramys* and a synapomorphy of the genus.

11. Curvature of anterior profile of P<sub>3</sub>. In lateral view, P<sub>3</sub> of *B. wakefieldi* and *B. brutyi* has a relatively straight (approximately vertical) anterior profile. In *B. triradiatus* and *B. parvus* the crown expands anteriorly to produce a curved profile. The sectorial P<sub>3</sub> of *Cercartetus* does not curve forward anteriorly (although the autapomorphic premolariform M<sub>1</sub> of *C. concinnus* does). Anterior curvature may be associated with increased P<sub>3</sub> size, with enlargement having been achieved by anterior extension of the crown. However P<sub>3</sub>s of *T. caunus* and *T. vulpecula*, which are curved, are smaller than those of *Spilocuscus* and *Phalanger*, which are less curved. Size and curvature are therefore not necessarily linked. It is possible that Miocene P<sub>3</sub>s represent primary enlargement of the tooth without the functional elaboration of other species, in which the inflated anterior edge may disperse stress, increase occlusal area, or perform some other function. A curved anterior profile is regarded as apomorphic within Burramyidae.

12. Lingual concavity/buccal convexity of P<sub>3</sub>. The P<sub>3</sub> blade of *Burramys* is concave lingually and convex buccally (particularly anteriorly). The contrast between lingual and buccal curvature is least pronounced in *B. wakefieldi* and *B. brutyi* and more pronounced in *B. parvus* and slightly more in *B. triradiatus*. As with anterior profile curvature, this feature occurs in *Trichosurus* but not in *Cercartetus*, *Spilocuscus* or *Phalanger*. It is regarded as apomorphic.

13. Arching of dorsal edge of P<sub>3</sub>. The dorsal edge of P<sub>3</sub> is arched in *B. parvus*; in the other species it is straight, but in *B. triradiatus* there is a slight curvature at the anterior end of the blade. The sectorial teeth of *Cercartetus* do not have a dorsal blade edge homologous with that of *Burramys* and so do not provide a useful comparison. The dorsal edge of P<sub>3</sub> is straight in phalangerids and this is assumed to be the plesiomorphic condition.

14. Divergence of P<sub>3</sub> from anteroposterior axis of molar row. In *Burramys*, the longitudinal axis of P<sub>3</sub> departs from the ramus such that it forms an angle with the anteroposterior molar row axis. This angle is largest in *B. wakefieldi* and is larger in *B. parvus* and *B. triradiatus* than in *B. brutyi*. In *Cercartetus* the longitudinal axis of the lower sectorial tooth is parallel to the anteroposterior axis of the molar row and within phalangerines, a more oblique placement of P<sub>3</sub> is regarded as apomorphic (Flannery et al., 1987). Divergence of P<sub>3</sub> from the anteroposterior axis of the molar row is a synapomorphy of *Burramys*; within *Burramys*, the plesiomorphic condition is taken to be a less divergent P<sub>3</sub>.

15. Transverse apical compression of P<sub>3</sub>. In anterior view, the crown of P<sub>3</sub> of *Burramys* tapers from the base, attenuating dorsally then terminating apically

with a serrated longitudinal median ridge. This transverse apical compression is least pronounced in the Miocene species and most pronounced in *B. triradiatus*. Crowns of the sectorial premolars of *Cercartetus*, *Trichosurus*, *Spilocuscus* and *Phalanger* are less attenuated than those of *Burramys*. Increased dorsal transverse compression is synapomorphic for *Burramys*. Laterally compressed P<sub>3</sub>s are regarded as more derived than those with thicker apices.

16. Distinction of talonid and trigonid of M<sub>1</sub>. In *B. wakefieldi* the talonid and trigonid of M<sub>1</sub> are clearly demarcated in occlusal view by lingual and buccal indentations. In *B. brutyi* and *B. parvus* the talonid and trigonid are less distinct. M<sub>1</sub> is not known for *B. triradiatus*. Talonids and trigonids are more distinct in *Cercartetus* than in *Burramys*, indicating the plesiomorphic state. The fused talonid and trigonid departs further from primitive tribosphenic morphology. Alternatively, the structure of M<sub>1</sub> in *B. wakefieldi* could be autapomorphic, with the crests defining the talonid and trigonid functioning primarily as buttresses for the anterolingual crests which may, in this animal, have extended the function of P<sub>3</sub>. However, the former hypothesis is preferred.

17. Lingual displacement of protoconid of M<sub>1</sub>. The protoconid of M<sub>1</sub> is displaced further lingually in *B. wakefieldi* than in *B. brutyi* or *B. parvus* so that in *B. wakefieldi* the crests associated with P<sub>3</sub> and the M<sub>1</sub> protoconid, metaconid and entoconid form an almost straight line. The position of the protoconid is variable in *Cercartetus* and phalangerids. In the primitive tribosphenic molar, the protoconid is a buccal cusp, so lingual displacement is regarded as apomorphic.

18. Anterior displacement of metaconid of M<sub>1</sub>. The paraconid is absent in *Burramys* and the most anterior lingual cusp is the metaconid. In *B. parvus* the metaconid is more anterior than in *B. wakefieldi* or *B. brutyi*, narrowing the gap in the P<sub>3</sub>-M<sub>1</sub> crest. In the Phalangeridae and *Cercartetus* position of the metaconid relative to the protoconid is variable. Outgroup analysis does not resolve the polarity of this character. The metaconid of *B. parvus* occupies the position that in a plesiomorphic (tribosphenic) molar would have supported the paraconid, so the anteriorly displaced metaconid is regarded as apomorphic.

Inclination of M<sub>1</sub> trigonid against P<sub>3</sub>. The trigonid of M<sub>1</sub> rises more steeply against the posterior face of P<sub>3</sub> in *B. brutyi* and *B. wakefieldi* than in *B. parvus*. Neither *Cercartetus* nor phalangerids give a clear indication of the polarity of this character. It has developed a number of times in phalangerids and pilkipildrids and is probably homoplasious.

19. Relative length of lower molars. M<sub>2-4</sub> of *Burramys* differ in their lengths (relative to widths) such that *B. brutyi* < *B. triradiatus* < *B. parvus*. M<sub>2-4</sub> are not known for *B. wakefieldi* but judging by their alveoli, they were of similar proportions to those of *B. brutyi*. In

*Cercartetus*, *Trichosurus*, *Spilocuscus* and *Phalanger*, the molars are relatively long, implying that this is the plesiomorphic condition.

20. Neomorphic cuspid at intersection of postmetacristid and preentocristid of M<sub>2-3</sub>. In *B. brutyi* and *B. parvus* there is usually a small neomorphic cuspid approximately half way along the lingual margin of the crown, at the junction of the postmetacristid and the preentocristid. This cuspid is not present in the few available lower molars of *B. triradiatus*, nor in *Cercartetus*, *Trichosurus*, *Spilocuscus* or *Phalanger*, suggesting that it is apomorphic in the Burramyidae.

Lingual cusps skewed ahead of buccal cusps of M<sub>2-3</sub>. In *B. triradiatus*, the lingual cusps of M<sub>2-3</sub> are ahead of the buccal cusps, skewing the sides of the teeth slightly. This skew is less evident in *B. brutyi* and slightly less again in *B. parvus*. *Cercartetus caudatus* is about as skewed as *B. parvus* and is the least skewed of species of *Cercartetus*, with *C. nanus* and *C. concinnus* showing about the same, increased degree of skew. The amount of skew on the molars is variable within phalangerids, ranging from very minor to quite pronounced. Outgroup analysis gives no clear indication of whether skewed molars are plesiomorphic or derived in *Burramys*.

21. Transverse loph(id)s of M<sub>2-3</sub> and M<sub>2-3</sub>. The transverse lophs and lophids of M<sub>2-3</sub> and M<sub>2-3</sub> are more complete in *B. triradiatus* than in *B. brutyi* or *B. parvus*, such that the central basins and the pre- and post-cingular basins of the teeth are deeper and more clearly defined in the Hamilton species. *Cercartetus* lacks transverse loph(id)s but this is probably apomorphic for the genus; lophs and lophids are well formed on the molars of the more plesiomorphic phalangerids. *Burramys triradiatus* is thought to be relatively plesiomorphic in possessing more complete molar lophs and lophids.

22. Number of roots M<sub>1-3</sub>. M<sub>1-3</sub> are double-rooted in *B. wakefieldi*, *B. brutyi* and *B. parvus*, but in *B. triradiatus* are 3-rooted. Turnbull et al. (1987) regarded the 3-rooted condition as a plesiomorphic retention. However, *Cercartetus*, phalangerids and virtually all marsupials have 2-rooted molars, making the plesiomorphic retention of 3-rooted lower molars by *B. triradiatus* seem unlikely. The 3-rooted lower molars of *B. triradiatus* are interpreted as autapomorphics.

23. Number of roots M<sub>4</sub>. M<sub>4</sub> is single-rooted in *B. parvus*, double-rooted in *B. wakefieldi* and *B. brutyi*, and has 3 roots in *B. triradiatus*. M<sub>4</sub> of *Cercartetus* (where it occurs) and phalangerids has 2 roots. The single-rooted and three-rooted M<sub>4</sub> of *B. parvus* and *B. triradiatus* (respectively) are interpreted as alternative apomorphic states derived from a 2-rooted plesiomorphic condition.

24. Reduction of M<sub>4</sub>. M<sub>4</sub> is most reduced in *B. parvus* and least reduced in *B. triradiatus*, with the Miocene

species intermediate. *Cercartetus lepidus* and *C. caudatus* (apparently the most plesiomorphic *Cercartetus*) have M<sub>4</sub>, though reduced; in *C. nanus* and *C. concinnus* M<sub>4</sub> is absent. In *Trichosurus* M<sub>4</sub> is subequal to M<sub>1-3</sub>; in *Spilocus* and *Phalanger* (which are generally more derived than *Trichosurus*) it is slightly smaller than the anterior molars. Reduction of the posterior molars occurs frequently and independently. Since primitive members of both outgroups have less reduced M<sub>4</sub>, and since reduction of the molar row posteriorly is commonly a derived state, more reduced M<sub>4</sub>s are interpreted as apomorphic. Although M<sub>4</sub> reduction correlates with M<sub>4</sub> root number in *Burramys*, it is treated as a separate character since, as demonstrated by the relative sizes and number of roots of M<sub>1-3</sub> in the different species, there is not necessarily a connection between molar size and number of roots.

25. Enlarged maxillary vacuities. Maxillary vacuities are larger in *B. parvus* than in *B. brutyi*. The vacuities of *Cercartetus* do not resolve this character. Vacuities are less extensive in phalangerids than in *B. parvus*, so a less evacuated palate is regarded as plesiomorphic.

26. Anterior limit of P<sup>3</sup> relative to zygomatic arch. P<sup>3</sup>, and therefore the anterior of the upper molar row, is further forward on the maxilla relative to the jugal portion of the zygomatic arch in *B. parvus* than in *B. brutyi*. In *C. concinnus* and *C. caudatus* the teeth are further forward than in *Burramys*; in *C. nanus* (and possibly also *C. lepidus*) the anterior extent of the teeth is similar to that in *B. parvus*. In *S. maculatus*, *P. carmelitae*, *T. arhemensis* and *T. vulpecula*, the cheekteeth commence further forwards. The polarity of this character is not immediately evident, particularly as there are a variety of states within *Cercartetus*: however the anterior disposition of the teeth in phalangerids would argue for that being the plesiomorphic condition.

Enlarged P<sup>3</sup> cingulum. The P<sub>3</sub> cingulum is slightly more developed in *B. parvus* than *B. brutyi* and significantly more pronounced in *B. triradiatus*. It possibly developed in conjunction with the enlargement of P<sup>3</sup> and the generation of greater bite forces at the P<sub>3</sub>s, functioning as a stopper for P<sub>3</sub> during premolar function (as indicated by posterolingual wear facets that stop abruptly at the cingulum in *B. parvus* and *B. triradiatus*) and also protecting the gums from hard food particles sectioned by the premolars. P<sup>3</sup>s of *Cercartetus* and phalangerids are not sufficiently similar to those of *Burramys* to have homologous cingulae, so outgroup comparison cannot polarize this character. If the enlarged cingulum is linked to P<sup>3</sup> size it is not an independent character.

Anterior attenuation of P<sup>3</sup>. In dorsal view, P<sup>3</sup> is more ovoid and in particular, more attenuated anteriorly, in *B. triradiatus* and in *B. parvus* than in *B. brutyi*. P<sup>3</sup> is insufficiently similar in *Cercartetus* and phalangerids to *Burramys* to be useful in determining polarity of this character. Anterior attenuation may be associated with

P<sup>3</sup> size and is probably linked to anterior inflation of P<sub>3</sub>; it is not treated as an independent character.

27. Posterobuccal rotation of molars rotate around maxilla. Upper molar row rotation is greater in *B. brutyi* than in *B. parvus*. The upper molars do not rotate buccally in a posterior direction in *Cercartetus*, but they do in phalangerids examined. Using *Cercartetus* as the primary outgroup and applying the principle of commonality, the rotating molar row of *B. brutyi* would be interpreted as more derived than the dental arcade of *B. parvus*.

Pronounced anterobuccal cingular basin M<sup>1</sup>. In *B. brutyi* there is a cingular basin on the anterobuccal corner of M<sub>1</sub>; in *B. triradiatus* there appears to be a narrow cingular pocket and in *B. parvus* the pocket is little more than a sloping cingular shelf. Inflation of the anterobuccal corner of M<sup>1</sup> is a synapomorphy for *Burramys*. It seems that the degree of definition of the anterobuccal pocket is inversely related to lingual shift of the paracone. Therefore, it is not treated as a separate character.

28. Inflation of lingual cusps of M<sup>1</sup>. No maxillary material is available for *B. wakefieldi*. In each of the other species of *Burramys*, the lingual side of M<sup>1</sup> is enlarged by a protoconule on the lingual margin, anterior to the protocone. Both protoconule and metaconule are more inflated in *B. parvus* than in other species and in association with this, lingual cusps of *B. parvus* lie closer to the lingual edge of the tooth than in the other species. There is no protoconule in *C. lepidus* or *C. caudatus*; it is present (relatively undeveloped) in *C. concinnus* and perhaps in a rudimentary state in *C. nanus*. There is no protoconule in *Trichosurus*, *Strigocuscus* or *Phalanger*. An enlarged protoconule is considered apomorphic.

29. Lingual displacement of paracone of M<sup>1</sup>. The M<sup>1</sup> paracone of *B. parvus* is displaced lingually so that the ectoloph is oblique with respect to the anteroposterior axis of the tooth. In *B. brutyi* and *B. triradiatus* the ectoloph is approximately parallel to the tooth axis, with the paracone more buccal. The M<sup>1</sup> paracone is not displaced lingually in *Cercartetus* or phalangerids, indicating that this is the plesiomorphic condition.

A Wagner analysis was performed using both ACCTRAN and DELTRAN algorithms of PAUP (Swafford, 1989). Wagner parsimony allows reversal or convergence to construct trees with the fewest steps. Where reversal or convergence would produce an equally parsimonious solution, ACCTRAN accelerates character transformations, favouring reversal, whereas DELTRAN delays transformations, favouring convergence (Wiley et al., 1991). Characters were ordered and a hypothetical ancestral *Burramys*, having all character states 0, was used to root the analysis.

ACCTRAN (Fig. 10) or DELTRAN optimisa-

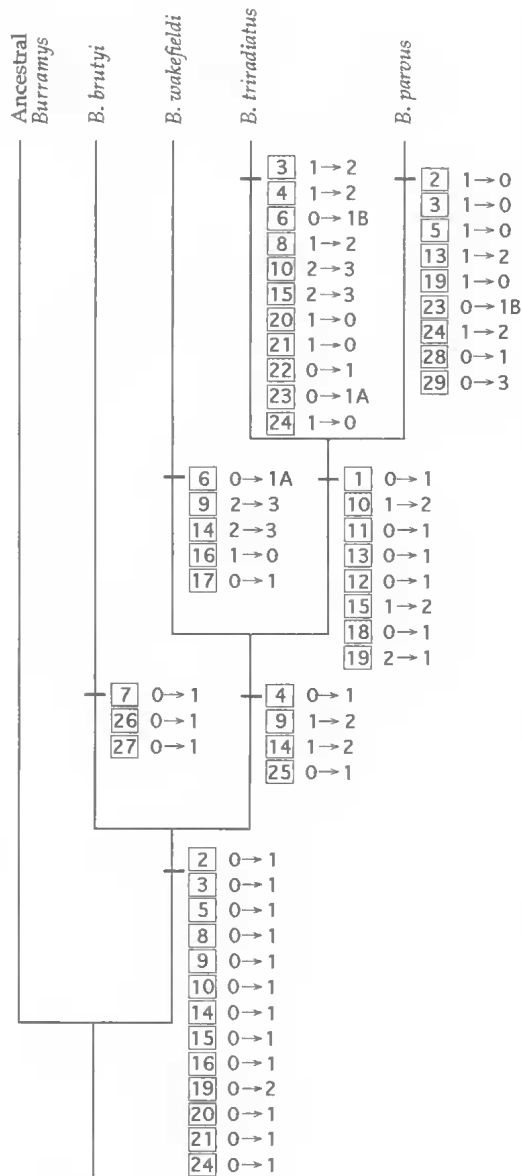


FIG. 10. A phylogenetic hypothesis of intrageneric relationships of *Burramys*. Apomorphies listed at nodes; character numbers in boxes refer to Table 5. Character state transformations indicated by arrows.

tion generated a single most parsimonious tree. The topology of this tree is identical for both algorithms. *Burramys parvus* and *B. triradiatus* form a clade to which *B. wakefieldi* is the plesiomorphic sister group; *B. brutyi* is the plesiomorphic sister group to a clade containing

all other species of *Burramys*. For some characters, the path of transformation differs depending upon whether transformation is accelerated or delayed. There are several convergent character states in the DELTRAN tree, no convergences and more reversals in the ACCTTRAN tree. When transformation is delayed the following character states arise convergently in *B. brutyi* and *B. parvus*: loph(id)s of M<sub>2-3</sub> reduce; neomorphic cuspid appears on M<sub>2-3</sub>; and M<sub>1</sub> talonid and trigonid become less distinct. Basal thickening of I<sub>1</sub> occurs independently in *B. brutyi* and *B. triradiatus*. The relative length of the lower molars decreases independently in *B. brutyi* and *B. wakefieldi*. With delayed transformation *B. parvus* reverses to a more plesiomorphic state of reduced robusticity and relatively long molars, and the relative size of M<sub>4</sub> in *B. triradiatus* increases secondarily. These reversals also occur when transformation is accelerated, as do the following: in *B. parvus* and *B. triradiatus* the relative length of lower molars increases (to a greater degree in *B. parvus*); in *B. parvus* the I<sub>2</sub>-P<sub>2</sub> interval increases; in *B. triradiatus* loph(id)s develop on M<sub>2-3</sub> and the neomorphic cuspid disappears from M<sub>2-3</sub>; and in *B. wakefieldi* the talonid and trigonid of M<sub>1</sub> are relatively distinct from one another.

Although a single most parsimonious tree was generated by this analysis, another tree only one step longer placed *B. wakefieldi* as the plesiomorphic sister-group of the other three species, and *B. brutyi* as the plesiomorphic sister-group of the *B. triradiatus* + *B. parvus* clade. A bootstrap analysis using a branch and bound search with 100 repetitions, to place confidence estimates on clades (from ACCTTRAN) found the node defining the *B. triradiatus* + *B. parvus* clade to be supported 84% of the time, but the node separating *B. brutyi* and *B. wakefieldi* occurred in less than 50% of repetitions. Using DELTRAN the *B. triradiatus* + *B. parvus* clade was supported 78% of the time, and the node separating the other 3 species from *B. brutyi* was supported by 55% of repetitions. In both cases, the node separating *B. brutyi* and *B. wakefieldi* is poorly resolved.

## DISCUSSION

*Burramys brutyi* is the only species of *Burramys* at Riversleigh and is not known elsewhere. It is represented by >150 specimens from 23 Sites in Systems A, B and C; it is one of the most widely distributed (spatially and temporally) marsupials at Riversleigh. Its earliest oc-

currence at late Oligocene (Myers & Archer, 1997) White Hunter Site is of similar age to the type locality of *B. wakefieldi* on Mammel Hill, Lake Palankarina, South Australia (Woodburne et al., 1993).

Metric analyses did not reveal any significant size variation between sites; variation within sites being as great as between sites. This persistence in unchanged form from the late Oligocene through much of the Miocene suggests an unusual degree of ecological stasis for the species.

Fossil *Burramys* in Victoria, South Australia and NW Queensland shows that small existing populations of *B. parvus* are remnants of a previously more diverse and far more widespread lineage, now apparently in decline. This fact urges particular conservation concern for the extant species. Although populations of *B. parvus* are apparently stable, they are threatened both by habitat disturbance and greenhouse warming, which could jeopardise their ability to survive (Geiser & Broome 1993).

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